THE UNIVERSITY OF ALBERTA

SOME SOCIAL ASPECTS OF FEEDING IN THE JAPANESE QUAIL

COTURNIX COTURNIX JAPONICA

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Some Social Aspects of Feeding in the Japanese Quail, *Coturnix coturnix japonica*" submitted by Patricia Frances Andrews in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Groups comprising four female Japanese quail were tested in various feeding Designs in which the food dishes were dispersed (Design I and II) or clustered (Design III) in a square cage, or clustered in a linear cage (Design IV).

The intensity of relationship between various measurements taken when the birds were fed in isolation was tested and a high correlation was found to exist between body weight change and amount of food eaten but not between time spent eating and amount of food eaten. I concluded that individual differences in body weight change were not ascribable to individual differences in defecation rate in my study as body weight change and number of feces per hour were not significantly correlated.

Groups were categorized on the basis of monarchial dominance being detected in them or not and the individual birds were categorized as being dominant or subordinate.

In Designs I and II presence of detectable monarchial dominance did not seem to have a deterring effect on the total amount of food eaten by the group whereas in Design III such an effect was found to be statistically significant.

There was no trend detected in the "food-dispersed Designs" for a monarchial dominant, i.e. a

despot in a monarchial hierarchy, to have a greater advantage over its subordinates with respect to body weight change and time spent eating, when these birds were feeding together than when they were feeding in isolation, whereas such a trend was noted in Design III. This was compatible with the data on reduced accessibility to food due to dominance in these Designs. In Designs I and II a despot did not reduce its subordinates' access to food to the same great extent that did a despot in Design III. This difference in results was attributed largely to the difference in the arrangement of the food containers (dispersed vs. clustered) in these Designs.

The results in this study indicated that, at least for groups in which monarchial dominance is not detected, Design IV is not a more competitive feeding situation than Design III.

Results on the level of agonistic behaviour in all these Designs suggested that there may be less tolerance exhibited in groups with monarchial dominance than in groups in which monarchial dominance is not detected.

Note: In all the Designs, the birds were subjected to 18 hours of food deprivation prior to the tests.

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INTRODUCTION

Domesticated *Coturnix* were either brought to Japan from China across the Korean Bridge about the 11th Century, or were domesticated in Japan at approximately this time (Howes, 1964). Although this species is a very good laboratory animal and adapts readily to a variety of laboratory conditions (Reese and Reese, 1962), only a very limited amount of behavioural research has been done on it and apparently nothing has been published on its feeding behaviour in group.

Ross and Ross (1949) found that when dogs were fed together, the positive effects of group feeding were expressed viz., the dogs ate more in group than in isolation. In their experiment a surfeit of food was presented in a large dish to dogs. No food dominance relationships were detectable. They suggested that if such conditions did not prevail, other effects of group may well be found.

In this research project, I studied feeding and related behaviour of Japanese quail in various situations involving different combinations and degrees of dominance, and increasing severity of food competition i.e., decreasing space and accessibility to food. In an attempt to evaluate the importance of these situations to a group's feeding and related behaviour, I was interested in investigating if these situations had a positive,

negative or no effect on some aspects of feeding i.e. if they increased, decreased, or had no effect on the amount of food eaten, body weight gain, time spent eating and level of expressed agonistic behavior.

METHODS AND DISCUSSION OF METHODS

Subjects, their raising and maintenance and assignment to Designs.

The birds used in the experiments were adult female Japanese quail. I chose females because they fight less than males (Kuo, 1960). Male quail are known to be vicious fighters in Southern China and once fighting has started it will not stop for serious injury but continues even to the point of exhaustion. I was afraid, therefore, I would have to disperse the food so much to reduce fighting in males in setting up the less competitive Designs, i.e. Designs I and II, that the positive effects of group would not be able to be expressed. Turner (1964) found evidence to suggest that the distance at which birds feed apart is an important factor in the expression of the "positive effects" of group on food consumption. However, in the more competitive Designs a stronger "negative effect" of group on its own food consumption probably would have been demonstrated if males had been used as subjects.

All the subjects were incubated in the laboratory and each hatch was raised together in groups of approximately 18 birds on a 14 hour daylength schedule (lights on from 8:00 am - 10:00 pm). The food used in testing and maintenance was Medicated Turkey Starter. Prior to the test weeks the birds were fed ad lib.

When a hatch was four weeks old I sexed the birds. As I arbitrarily decided to have groups of four females in my tests, I automatically eliminated the males from the group and chose the four females to comprise a test group by using the Table of Random Numbers. I decided to have four birds comprise a group as I wanted to be able to record accurately the time each individual bird spent eating and also the interactions occurring between the birds. Another reason for using four birds was that I also, theoretically at least, wanted them to have the opportunity to feed far away from each other in Designs I and II and therefore I put food in every corner of the square cage (see description and discussions of Designs I and II).

When the birds in a test group were eight weeks old I assigned the group to one of the feeding Designs and tested it. Each group was tested in only one Design but there were several replicates in each Design. I assigned the first three groups to the Designs in the following chronological order I, III, IV respectively,

as I wanted to get an estimation of how valid my hypotheses had been and, if necessary, change my Designs in function of the results obtained. I assigned the rest of the groups with one exception to the Designs by using the Table of Random Numbers so as to eliminate sampling bias. The one exception is Group 10 which I purposely assigned to Design III so that the results on amount of food eaten in the Design could be tested in a factorial analysis.

Thus the process of randomization was used to select four birds to comprise a test group and it was also employed to assign a majority of the groups to the Designs.

General procedure during test days

In most cases the subjects in each group were tested six days in the group situation and five days in the isolation. One exception to this was Group 10 which I tested seven days in group and six days in isolation, since I did not record the results of this Group's first test day in group or its first test day in isolation. I did not record the results of these two test days because some of the food containers I had to use on these days were not similar in size or shape to those used in all the other tests.

For the 11-day testing period I consecutively alternated a group of birds between the group and isolate

situation (visual isolation) daily in a particular feeding Design and these days were designated as Test Day 1 in group, Test Day 1 in isolation, Test Day 2 in group, Test Day 2 in isolation etc. I imposed this schedule so that the isolate situation would act as a control for the group situation. A number of workers used this technique to reduce variability. The major disadvantage of this technique is that the experience of undergoing one of the treatments may change the animal so greatly that it cannot be tested again under another treatment. I do not think that this was true in the case of alternating the birds between group treatment one day and isolate treatment the next. I had an ordered pattern of putting the birds in the group situation on every second day so as not to upset their social hierarchy by isolating them for too long a period. One possible disadvantage of this ordered pattern is that the birds might become conditioned to the rhythm, and the group feeding situation might be biased because the birds "anticipate" being fed in isolation every second day, or vice versa. If, for example, they eat less in group and more in isolation (or vice versa) towards the end of the eleven testing days as compared with the beginning of the tests, it may be that they are becoming conditioned to the rhythm. However, another interpretation of this is the "familiarization effect"; that is the birds are becoming more familiar with the group and isolate test situation and consequently may eat

more in either group or isolation because they are less emotional in the later tests or exhibit less exploratory behavior or both. I tested the birds for 11 consecutive days just in case stopping the tests over the weekend might have some undesirable disruptive influence on any trend that might be developing.

Although the "isolate test cages" appeared to be identical, their positions were not as they were arranged adjacently to each other, and so to eliminate any bias due to the different positions as well as unknown differences of the cages, I assigned each bird to an isolate cage by making use of the Table of Random Numbers.

Tolman (1965) found that "social facilitation" of feeding behavior of five and six day old chicks was optimal in the area of six hours of food deprivation and only minimal if existant for 0, 12, 24 hours of food deprivation. Tolman interpreted these results in terms of the "behavioural interaction hypothesis". At 0 - hours the rate of eating by the chicks is low enough to be increased but too low to be stimulating to a companion. "At around 6 - hours the rate is low enough to be increased and high enough to be stimulating. At the later hours, the rate is high enough to be stimulating but too high to show any increase." Tolman (1965).

As a pilot test I used 6 - hours food deprivation on a group that I assigned to Design I. My results indicated that the birds obviously did not feed more in

group than in isolation:

Mean amt. eaten in group for 1 hr. test = 5.56 g. $S\bar{x}$ 0.24 n=5

Mean amt. eaten in isolation for 1 hr. test = 6.84 g. $S\bar{x}$ 0.35 n=3

I then thought that maybe at six hours food deprivation the birds' rate of eating was too low to be stimulating to each other. So two days later I deprived this group of food for 12 hours and fed them in isolation for the one hour test. With this period of deprivation the birds ate 6.45 grams which is less than the mean amount of food eaten in isolation with 6-hours food deprivation. So the next day I used an even greater period of deprivation, 18 hours, and fed the birds in isolation. They consumed 7.35 grams during the one hour test. This period of food deprivation was not so great that the birds ate during the whole test period in isolation so that when they were put in group any "positive effects" of the group on food consumption would not be detected. I therefore chose 18 hours of food deprivation for the tests.

I decided to have the one hour test period from 9:00 - 10:00 am as I knew there would be disturbances in my laboratory after that time in the fall when I would be still conducting tests. I could not have the test period earlier than 9:00 am as the lights went on at 8:00 am and there were preparations for the test that I could do only just before which took me approximately one hour. As a pilot test to evaluate the possible importance of time of day on amount of food eaten I recorded the amount two

groups ate at different times during the day and the period from approximately 9:00 - 10:00 am was not a period when food consumption was decreased as compared with other times of the day.

I removed the water from the cage during the test periods, as I wanted the birds' body weight gain to be ascribable only to food intake and not water intake.

Outside the test period, each group was kept in cages similar to those used in the test.

To facilitate individual identification I tagged each bird with a different colour tag and tinted the breast, back, and neck of each bird with a different colour marking pencil.

Measurements taken during the test periods

Amount of food eaten

The amount of food consumed during the test was obtained by subtracting the weight of the food plus food containers before the test period from that after the test period. Weighings were made on a Stanton Balance and readings were taken to the nearest one hundredth of a gram. A food container filled with food not used in the test was also weighed before and after the test to serve as a control. Thus food weight loss or gain due to atmospheric humidity could be obtained.

Body weight change

Body weight change of the birds was measured by weighing the birds before and after the test period. A Mettler balance was used and estimates were made to the

nearest hundredth of a gram. A basic order was used in the weighing procedure of the birds such that the bird which was weighed first on Day N of group and Day N of isolation was weighed last on Day N + 1 of group and Day N + 1 of isolation. Thus if a bird gained more weight than the others in a group after the one hour test, this could not be attributed to this bird's always being weighed first.

I recorded the change in body weight after each test period to establish whether it were a good index of the amount of food eaten. To test this I calculated a correlation coefficient in which I used the means of all the individual birds' body weight changes and amounts of food eaten during the five test periods in isolation (Table 2, page 37). If body weight change were a good index I would use it then as an estimation of how much the individual birds ate when they were together in group by extrapolation from a regression line calculated by the method of least squares.

Time spent eating

I recorded as well time spent eating by each bird. I did this by direct observation and used a Rustrak Multichannel Recorder which I operated manually.

Because towards the end of my project I was pressed for time, I tested two groups at once, testing one group in isolation while the other was being tested in group. When I did this, I could only observe one of the groups

during the test period so I observed each group only when it was in the group situation. This was the case with Groups 3, 6, 8 and 10. Therefore, I do not have data on the time spent eating in isolation for these Groups.

I also tested whether time spent eating were a good index of amount of food eaten by computing a correlation coefficient as I did to test body weight change.

Number of defecations

I recorded the number of defecations during the one hour test to ascertain whether individual differences in defecation rate were involved in individual differences in body weight change. I also tested this by calculating a correlation coefficient as I did for body weight change.

Basal metabolism, nervousness, ambient temperature and level of interactions between birds

Since basal metabolism, nervousness, ambient temperature, and level of agonistic interactions are all variables which could possibly affect feeding behaviour, I attempted to evaluate them to assist in the interpretation of the results.

Basal metabolism

In estimating the individual bird's basal metabolism, the weight-metabolism regression coefficient of each bird were calculated (Table 4, page 40).

For non-passerine birds this is computed by raising the body weight in Kg. to the 0.723 power. (Lasiewski and Dawson, 1967). Body weights of the birds at the beginning of their first test in group were used.

Nervousness

I had noted that nervous birds consistently popped up and hit their heads against the top of their cage whenever I approached them, and I used this behaviour as a criterion for nervousness.

Ambient temperature

I recorded the temperature of the room about five minutes before the test period began, as ambient temperature can have an effect on feeding when it is outside the thermoneutral range of the birds. The temperature record is tabulated on page 42.

Interactions between birds

I recorded, as well, the interactions that I observed during the test periods between all the birds in each group. The type of interactions I noted were mainly those which I interpreted as agonistic. Agonistic behaviour is defined by Scott (1965) as "behaviour associated with conflict or fighting between two individuals".

Agonistic behaviour is a kind of behavior which involves a number of components such as competition, expression of dominance, hormones and unknown factors. Therefore, what I measured when I estimated the level of

agonistic encounters was the resultant of many factors known and unknown. In the discussion of my results I will attempt to evaluate how the components dominance and degree of competition were involved. I will, at this point, discuss these two components.

Competition

Depending on the situation, animals may compete for a number of incentives in their environment such as food, space, mates. By increasing competition, tolerance within a social group may be decreased with a resultant increase in aggressive behaviour. Food competition need not necessarily involve dominance. Two strange birds deprived of food, when fed together display agonistic behaviour. In the absence of fixed dominance in chaffinches, the hungrier bird always drove the others from the food dish and defended it (Marler 1957). However, competition for food can involve dominance, and if intense may increase the expression of dominance. "Balance between fear of despots and degree of hunger is an important element in food competition, at least, as seen in the laboratory. Chickens that have been strongly persecuted learn not to come to the food hopper until the dominant birds have finished eating" (Collias, 1944). Subordinate birds, however, show a greater readiness to approach the dominant individuals at the food when they are starved. Increased frequency of fighting results (Marler, 1956). Among chimpanzees, extreme food deprivation by

itself may not be sufficient cause for a subordinate to respond positively in food competition with a dominant animal unless there is high expectancy of success (Nowlis, 1941). Thus, an animal could be aggressive but its aggressiveness is inhibited in the presence of strong dominance. So a competitive situation may increase the level of aggressiveness of all individuals uniformly or it may have a more differential effect and increase the level of aggressiveness in the dominant only.

The possible effects of the Designs on competition will be discussed in the section on Designs.

Dominance

"Social dominance refers to the determination of behaviour of given individuals by other individuals whether by aggressive behaviour or by other means" (Collias, 1944). In a dominance-subordination interaction, Scott (1965) describes the behaviour of both individuals as agonistic. That of one individual consists of actual fighting or its substitute e.g. threat; while that of the other individual consists of challenging, retaliating, remaining passive or attempting to escape. Many, many factors affect dominance or its expression such as seniority, previous experience, hormones, body weight, skill in encounters and age.

There are a number of basic types of hierarchies in which dominance may be expressed. A "peck-right" system is based on unidirectional dominance and each bird

is ranked according to the number of individuals in the group that it may dominate without retaliation. The order may be straight-line, A pecks B, B pecks C ($A \rightarrow B \rightarrow C$) or have a geometrical pattern composed of "pecking triangles" ($A \rightarrow B \rightarrow C \rightarrow A$).

Another system which is based on unidirectional dominance is the monarchial system. Collias (1944) described a monarchial type of social order as one in which one bird, the despot, tends to inhibit aggressive relations between his subordinates.

Bidirectional dominance (formerly designated as "peck-dominance") exists when individuals exchange pecks but one of each contact pair consistently gives more pecks than it receives and this is the dominant of the two (Bennet, 1939).

Howard Farris (1964) reported observing expressed monarchial dominance in three groups of Japanese quail that had been reared together from hatching (two groups comprised 18 birds each, one group 6 birds). In the two groups of 18 birds Farris sexed the tyrant, and in one case it was a male and in the other a female. When he removed the male tyrant, another male took over its role and when he removed the female tyrant, no other bird assumed the absent tyrant's dominant role.

Selinger, Howard and Bermant (1967) reported that paired male Japanese quail mutually exchanged pecks, with one male giving more pecks than the other. Sachs (1966)

paired eight male Japanese quail in 49 two-minute encounters in an incomplete round robin. The results of these 49 encounters yielded a straight line peck order.

Originally when this study was designed, my aim was to emphasize the effect of Design on the amount of food eaten, and not to particularly study dominance as a variable. Therefore the process of randomization was employed in selecting the groups and assigning them to the Designs to average out any effects of dominance in the Designs, so that no additional uncontrolled factor due to dominance would be introduced in any one of the Designs. Randomization is one effective technique to accomplish this if a "continuous" hierarchial system is present, wherein the difference between the hierarchies of any two groups in the species is not very great. As I proceeded with my study, I discovered that such a system was not characteristically present in my female quail. Frequently what appeared to occur was that which approximated a discontinuous system with the gap between hierarchies with and without detectable monarchial dominance being considerably great. When I realized this I was then extremely interested in dominance as a variable in itself, as it added a very exciting and original dimension to my problem. It would have been most interesting to study the effect of Designs, feeding condition whether in group or in isolation, and dominance with its two levels, presence and absence of detectable monarchial dominance,

as well as the interactions of all these main effects in a factorial analysis. However, the most effective way of assuring that the two levels of dominance are represented in each Design would be to select the groups beforehand and assign them to the Designs not at random. But since I had already randomly selected some of my groups and assigned them to the Designs at random and run the tests, I thought it advisable not to change this method in the middle of my project. Thus I did not have all the necessary interactions of the main factors to make it possible to do this factorial analysis. Therefore, when I investigated the effects of dominance in this study it was not in the most efficient way possible.

Evaluation of dominance

I attempted to evaluate dominance at the individual level by intra-group comparison of the individual birds; and at the group level, I categorized each group with respect to presence or absence of detectable monarchial dominance.

In my attempt to evaluate dominance at the individual level, I computed what percentage each bird in a given group contributed to the total number of agonistic encounters occurring in that group during all the test periods (Table 6, page 46), i.e. what percentage each bird contributed by being the aggressor in encounters or contributed by being responsible for agonistic encounters occurring as in an avoidance encounter or both.

If Bird A pecked another bird, I would then add one to Bird A's score of contribution to the general level of agonistic behaviour in the group. If a subordinate bird "gave way" to the dominant, I would count that agonistic encounter among the dominant's contribution.

In an attempt to evaluate dominance at the group level, I arbitrarily established two general categories: (1) groups with clearly detectable monarchial dominance; and (2) groups without clearly detectable monarchial dominance (Table 7, page 47). This second category was to include both groups with dominance other than monarchial type present, as well as groups with no dominance order exhibited at all.

If I observed that the dominant bird contributed at least 95 per cent to the total number of agonistic encounters occurring in the group during the tests, and if that dominant bird consistently lost none of the agonistic encounters in which it was involved, i.e. its dominance was unidirectional, I would consider that established monarchial dominance was clearly expressed in that group. If these conditions were not met during my observations throughout the test periods, I would put that group in the class where expression of established monarchial dominance was not clearly detectable.

Evaluation of the importance of dominance on feeding and related behaviour

I was then interested in studying whether dominance had any effect on various aspects of feeding and related behaviour viz. accessibility to food, amount of food eaten, body weight change, time spent eating and expressed level of agonistic interactions. If dominance did have an effect, I was also interested in whether this effect was influenced by the Designs. I will now discuss how I attempted to investigate and test this.

Dominance and reduced accessibility to food

To evaluate dominance and reduced accessibility to food, I tabulated for each group the mean frequency one bird displaced another or prevented another from reaching the dish (Table 8, page 48). The dominant in each group was compared with the subordinates in this table to see if it was the dominant that was most frequently responsible for reduced accessibility to food as emphasized by agonistic interactions if such reduced accessibility did exist. Also the Designs the groups were in, as well as the dominance category, i.e., presence vs. absence of detectable monarchial dominance, were recorded to see the possible influence, if any, of each. In a further attempt to evaluate reduced accessibility of food due to dominance, I tabulated the ratio—mean number of times a subordinate in a group gained successful access to food: mean number of times a subordinate was prevented

accessibility to food (Table 9, page 50). I arbitrarily defined successful gain of access to food as the subordinate's reaching the food container and not leaving it for at least up to approximately five minutes because of some obvious action on the part of the dominant. I did not directly record the number of times a subordinate gained successful access to food, but I obtained such information by inference, as I did record for most of the groups the position of all the birds in the cage approximately every five minutes, and also at what time one bird displaced another or prevented another from reaching the food dish. I did not record this for Groups 6, 8 and 9.

Dominance and amount of food eaten

I was interested in investigating whether presence or absence of detectable monarchial dominance affected food consumption of the group as a whole and if so, whether this influence of dominance was modified by Design. In attempting to establish this, I estimated the influence of various groups on their respective food consumption by using the amount each group ate in isolation as a control (Table 10, page 51).

It would have been interesting to study kind of dominance expressed, Designs and feeding condition in a factorial analysis of variance. However, as previously discussed (page 15), I did not realize that I would be

interested in dominance as a variable and therefore I do not have enough interactions of all the levels of the main factors to make this feasible.

Therefore, in the Designs where I do not have two groups with detectable monarchial dominance present as well as two groups with such a dominance not detectable, I was not able to do a statistical test, so instead I described the behaviour in a non-statistical way. In Design III, however, where I do have four such groups, I was able to do a factorial analysis of variance, to test for significance, the effect of the interaction, type of dominance expressed X feeding condition, i.e. the Dom X I interaction, on the amount of food eaten (Table 11, page 52). Since I did not record the results of Test Day 1 in group and Test Day 1 in isolation for one of the groups (Group 10) in this Design, I omitted the results of these days for the other groups in the factorial analysis.

Dominance and body weight gain

I wanted to compare the body weight change of the dominant bird with that of its subordinates in each group after the one hour feeding tests. I first estimated this roughly by comparing the means of the individual bird's body weight change in each group over all the tests and noting whether the dominant appeared to gain more weight than the subordinates (Table 12, page 54). If the dominant did, I tested whether the difference was significant.

The data for each group which I was testing for significance were considered as a repeated measurement design with one factor A, rank of bird, assigned between subjects with two levels, dominant and subordinate. Two factors assigned within subjects were (1), G, feeding conditions with two levels group and isolation and (2) D, days with 5 levels which were nested within each feeding condition. Another main factor was P with two levels pre and post weight of the bird. Thus a significant A X P X G interaction indicated that the dominant gained significantly more weight than its subordinates and that this difference was significantly influenced by the feeding condition. The data were analysed by an unweighted means solution for unequal number of subjects, since only one bird was in the first level of A, i.e. the dominant category, and three birds were in the second level of A, the subordinate category. The results of these analyses are on pages 55-59. In the discussion of these methods, the validity of this statistical treatment used was questioned due to the use of preimposed conditions.

In Design III, I concluded the results of Group 7 and Group 10 in the one factorial analysis (Table 16, page 58), since detectable monarchial dominance was present in both of these groups and thus they could be considered replicates. As I did not record the results of the first test day in group and first test day in isolation for Group 10 (page 4), to avoid complication, I excluded the results of these test days for Group 7 from the analysis.

When I interpreted the results of these comparisons of dominant vs. subordinate body weight change I took the possible effects of Designs as well as kind of dominance expressed into consideration.

Dominance and time spent eating

I also compared the amount of time spent eating by the dominant in each group during the tests with that spent by its subordinates (Table 18, page 60) and used a similar factorial analysis to test differences for significance, as that used for body weight change. One modification of this factorial design for time spent eating was that it did not have, of course, the main factor P (pre and post weight) to be considered. Other modifications were in the analyses of Group 6 and 10 where no data on time spent eating was recorded in their isolation tests (see page 9) and therefore neither the main effect G (feeding condition, whether in group or isolation) nor its interactions with the other main effects could be analysed. In the analysis of time spent eating for Group 1 only results from group and isolation Test Days 1, 4 and 5 could be considered. This was because time spent eating during the Third Test Day in group and the Second Test Day in isolation could not be recorded for this group, since the Rustrak recorder was not in working order on those days.

The results of these "dominant vs. subordinate time spent eating comparisons" were interpreted by taking

into consideration the possible effects of Design and kind of dominance expressed.

Presence vs. absence of monarchial dominance and level of expressed agonistic behavior

I was interested in the level of expressed agonistic behavior in groups where detectable monarchial dominance was present relative to that in groups where it was absent and made an intra-design comparison of these two dominance categories to study this. I also made an inter-design comparison of each dominance category to investigate whether Design had an influence on the level of expressed agonistic behavior.

I attempted to evaluate the level of agonistic encounters expressed in each group by recording the number of pecks and other agonistic encounters occurring during the test periods. Under the general term other agonistic encounters I included: interrupted peck, intention movement of peck, threat posture, charging, jumping, chasing, feather pulling, leg pulling, pushing, "head turn", vocal threat, giving way and other avoidance reactions. I then computed the means of the total agonistic encounters that occurred in the groups during the test periods and also the number of tests when no agonistic encounters were observed at all (Table 27, page 68).

Supplementary tests

To facilitate the interpretation of some of my results, a number of supplementary tests were made. The methods and results of these are recorded in the Appendix (pages 95-105).

Designs

In the Designs a number of variables were involved that could possibly affect feeding behaviour. They are: quantity of food, distribution and accessibility of food, space; group characteristics such as: nervousness of the birds, metabolism, level of agonistic behaviour related or not related to dominance, as well as unknown variables. Quantity of food, distribution and accessibility of food, and space were fixed variables in each Design. However, the groups' characteristics: nervousness of the birds, metabolism and level of agonistic behaviour were variables which I originally did not intend to study and so I relied on the process of randomization to balance out any bias they might introduce in the Designs. It is possible that all these variables can interact to have an effect on feeding behaviour and also have an effect on each other. This will be considered in the discussion of the results.

In Designs I, II and III, because of my small laboratory space, I found it necessary to house the birds in cages of one square foot on isolate testing days whereas I kept them in a four foot square cage on group testing

days. Because of reduced cage size associated with the isolate situation, I reduced the number of food containers so that the ratio of food containers to cage space would not be so much greater in the isolate situation as in the group.

In Tolman's experiment on social facilitation of feeding behaviour in the domestic chick (1964), a large compartment with two food cups was consistently associated with the paired condition whereas a small compartment with one food cup was consistently associated with the isolate condition. He then did another experiment to attempt to answer the question: Does the size of the compartment and number of food cups have an effect on daily cumulative weight gain? The results of the experiment indicated that they do not.

As a pilot experiment to see if Tolman's results applied to my quail and the conditions of my study, I alternated an isolated bird, Bird X, between the large group and small isolate cages with eight food containers and one food container respectively every day. I measured the amount of food eaten per hour at various given times during each day. I repeated this with another isolated bird, Bird Y. The results (Table 1) indicated that the size of the group cage and extra food containers apparently did not significantly increase the amount of food eaten by either of the two isolated birds.

Table 1 Comparison of amount of food eaten in grams by isolated birds in group cage, eight food containers present with amount eaten in isolate cage, one food container present

Bird	$\bar{X}$ amt. of food eaten in group cage with 8 food containers	$s_{\bar{x}}$	n*	$\bar{X}$ amt. of food eaten in isolate cage with 1 food container	$s_{\bar{x}}$	n*
X	1.14	± 0.18	7	1.19	± 0.19	7
Y	0.79	± 0.10	9	0.92	± 0.24	9

* n = Number of observations on given bird

I ended up using four containers in this Design in the isolate situation as I was afraid that by having one food container I might not place it in a bird's preferred corner, if the bird had one, and thus, I would introduce a bias into the isolate situation which was not present in the group situation.

Design I: Eight food containers dispersed, square cage

When the birds were tested in group there were eight food containers arranged as diagrammed in Figure 1, page 32 in the group test cage. Thus the same quantity of food was present as in Designs III and IV.

In the isolation situation there were four food containers, one placed in each corner of the isolate test cage.

In Design I the aim was to provide a situation where the effects of competition and the expression of dominance (if present) were not favoured. My hypothesis was that any negative effects of a group on its own food consumption when feeding together, would be minimized. I also hypothesized that the level of agonistic behaviour at the group and individual level would be less in this Design than in more competitive ones.

Marler (1956) suggests that defence of the food area by a dominant chaffinch is merely defence of the tolerance distance about it and when it is near the food, the food is included in the "tolerance distance" which it defends. Therefore, when I was setting up this Design, I

dispersed the food just in case the foregoing point were applicable to my quail. Thus an attempt was made to provide the subordinate birds with the opportunity to feed outside the tolerance distance of the dominant. In my pilot observations I noted that a subordinate bird could feed without interruption from the dominant if the former were feeding apart from the latter at another corner of the cage. I put two food containers in every corner so that the opportunity would also be provided for any two birds to be able to feed close together. Turner (1964) concluded that in chaffinches a feeding actor will induce a reactor to feed and this inducement to feed (i.e. "social facilitation") is more powerful if the actor's feeding activity takes place in the vicinity of the reactor's food. This he interpreted as local enhancement.

It was assumed that in this Design the social competition would be low enough not to produce any decrement in food consumption but high enough to allow "social facilitation" to occur.

<u>Design II: Ten food containers dispersed, square cage</u>

On the group test days there were ten food containers in the birds' cage as diagrammed in Figure 2, page 33. In the isolate days five food containers were put in each isolate test cage (Figure 3, page 34).

The aim in Design II was to provide a situation which de-emphasized the effects of competition and dominance to an ever greater extent than in Design I, and I hypothesized that any negative effects of a group on its own food consumption would be further minimized in this Design. In Design I, I noted that the birds spent more time in the back of the cage and ate more from the food containers at the back of the cage. This was probably due to the fact that the side of the cage at the front was of wire mesh and was exposed to the observer and other possible visual disturbances outside the cage, whereas all the other sides were of plywood, thus if the birds fed at the front of the cage they possibly could see that they were closer to the observer. At any rate, on the basis of this tendency to feed at the back of the cage and on the basis of results of Supplementary Test No. 1 (page 96), I put two extra food containers at the back of the cage, and thereby increased the quantity and accessibility to food as compared to that in Design I. I assumed that this Design would favor the positive or, at least, neutral effects of group on food consumption. More opportunity for local enhancement was provided as there were more food containers placed closely together and birds were able to feed near each other. However, it was also possible for a subordinate bird to escape from a dominant and still be able to feed, as some food containers were placed far apart.

Design III: Eight food containers clustered, square cage

In the group situation eight food containers were clustered together in the far right hand corner of the cage and in the isolation situation there were four food containers in the far right hand corner (Figures 4 and 5, page 35).

The aim in this Design was to favor competition and reduced accessibility to food. Accessibility to food was reduced in two ways. One way was the actual physical restriction imposed by clustering the food containers together. The second was by providing a situation where the influence of dominance could reduce accessibility to food. Since the food containers were clustered it was possible for the dominant to defend them. Also even if active defence did not occur the mere presence of the dominant at the food area could reduce other birds' accessibility as there was only one source of food in this situation. Nevertheless, multi-directional approach and retreat from the one source were still possible as a square cage was used in this Design.

I hypothesized that a given group would tend to eat more in the isolate than in the group situation in this Design. Since the food was clustered, it seemed that the probability of interactions, especially agonistic, occurring between birds would be higher in this situation due to crowding at the food source, unless the birds took turns feeding. If the former were the case, I hypothesized

that the level of agonistic behaviour would be greater than in Design I and II.

Design IV: Eight food containers localized, linear cage

The cage which was used for both the group and isolate situations was a "linear" cage 4' 7" x 4" x 10". Eight food containers were used for the group and four for isolation situation. They were clustered together as diagrammed in Figures 6 and 7, page 36.

The aim was to make Design IV the most competitive of all the Designs and one where reduced accessibility to food was most emphasized. Accessibility to food was more greatly reduced in this Design than in Design III. The physical restriction was greater since the reduced width of the cage forced one bird to be very close (at or almost at the point of contact) if it passed another in this cage. This Design also offered greater possibilities for reduced accessibility to food as emphasized by dominance, since in this Design "successive" rather than "simultaneous" defence was possible. A defending bird could drive the others away one at a time as only unidirectional approach and retreat were feasible.

I hypothesized that this situation would maximize any negative effects a group might have on its own food consumption and that level of agonistic behaviour would be greatest of all in this Design, unless the birds took turns feeding. Maximum difference between a dominant and a subordinate was also expected.

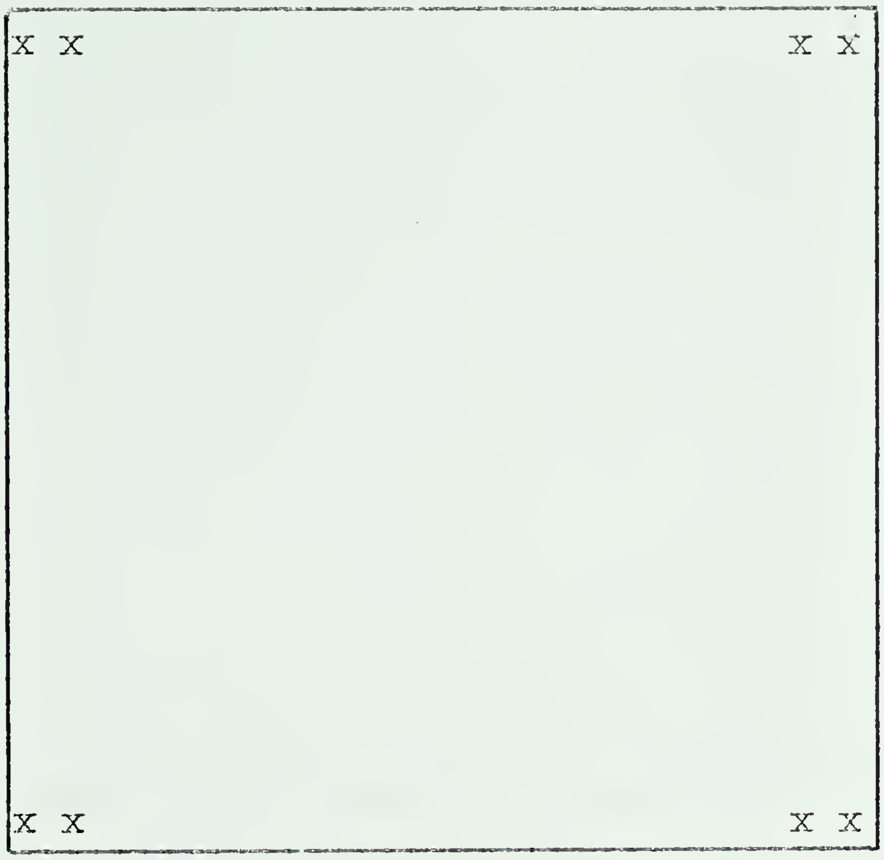

Figure 1 Arrangement of Food Containers in the Group Situation in Design I

(not drawn to scale)

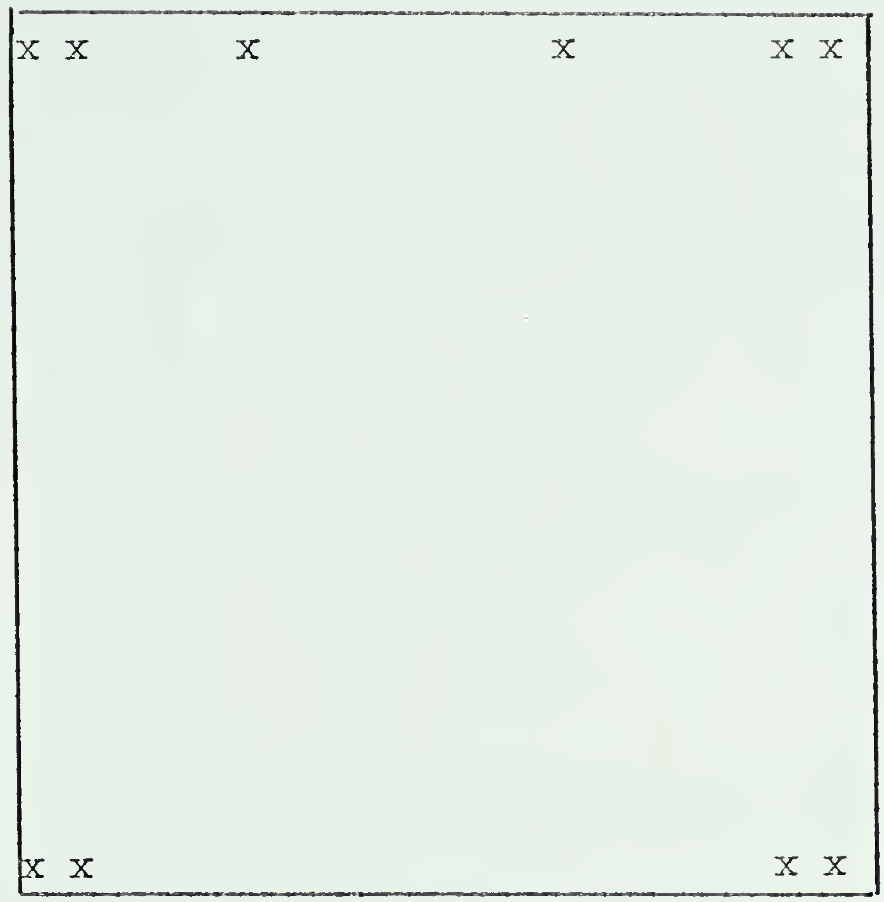

Figure 2 Arrangement of Food Containers in the Group Situation in Design II

(not drawn to scale)

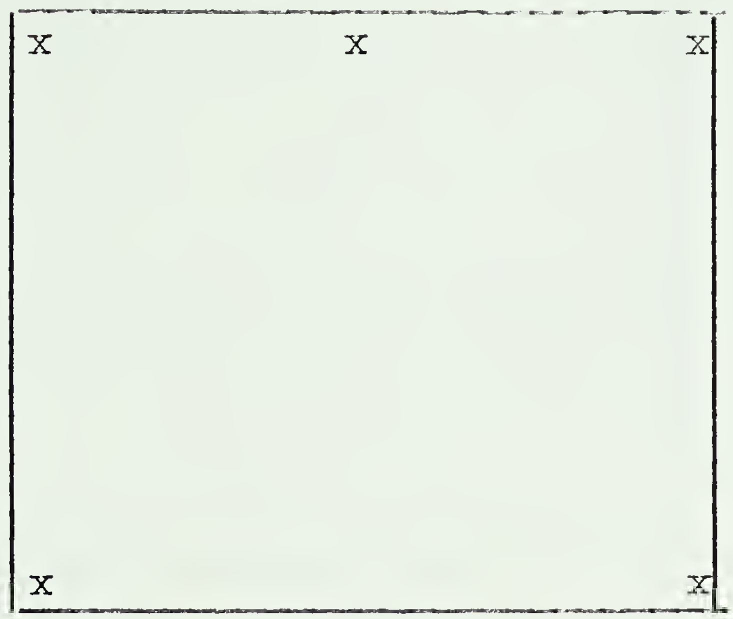

Figure 3 Arrangement of Food Containers in the Isolate Situation in Design II

(not drawn to scale)

Figure 4 Arrangement of Food Containers in the Group Situation in Design III

(not drawn to scale)

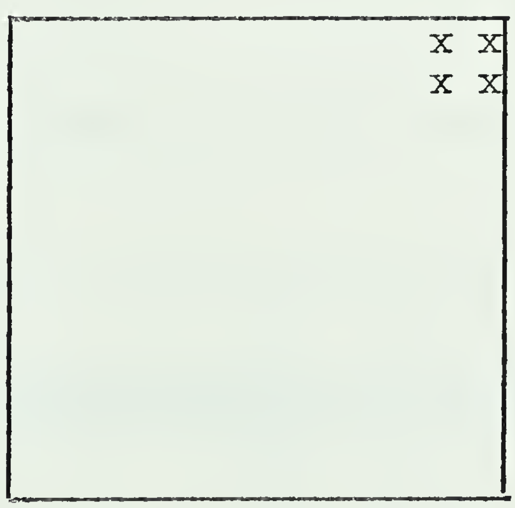

Figure 5 Arrangement of Food Containers in the Isolate Situation in Design III

(not drawn to scale)

Figure 6 Arrangement of Food Containers in the Group Situation in Design IV

(not drawn to scale)

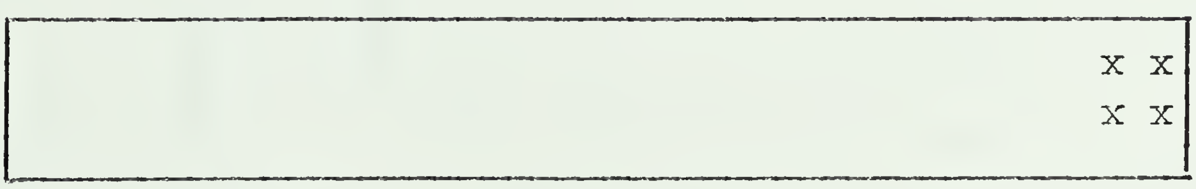

Figure 7 Arrangement of Food Containers in the Isolate Situation in Design IV

(not drawn to scale)

Results

Table 2 Degree of relation between some of the variates measured

Variates tested	Correlation coefficient	Coefficient of determination	No. of pairs of observations
Body weight change and amount of food eaten	0.96	0.92	44
Time spent eating and amount of food eaten	0.52	0.27	24
No. of feces / hr. test and body weight change	0.21	0.04	40

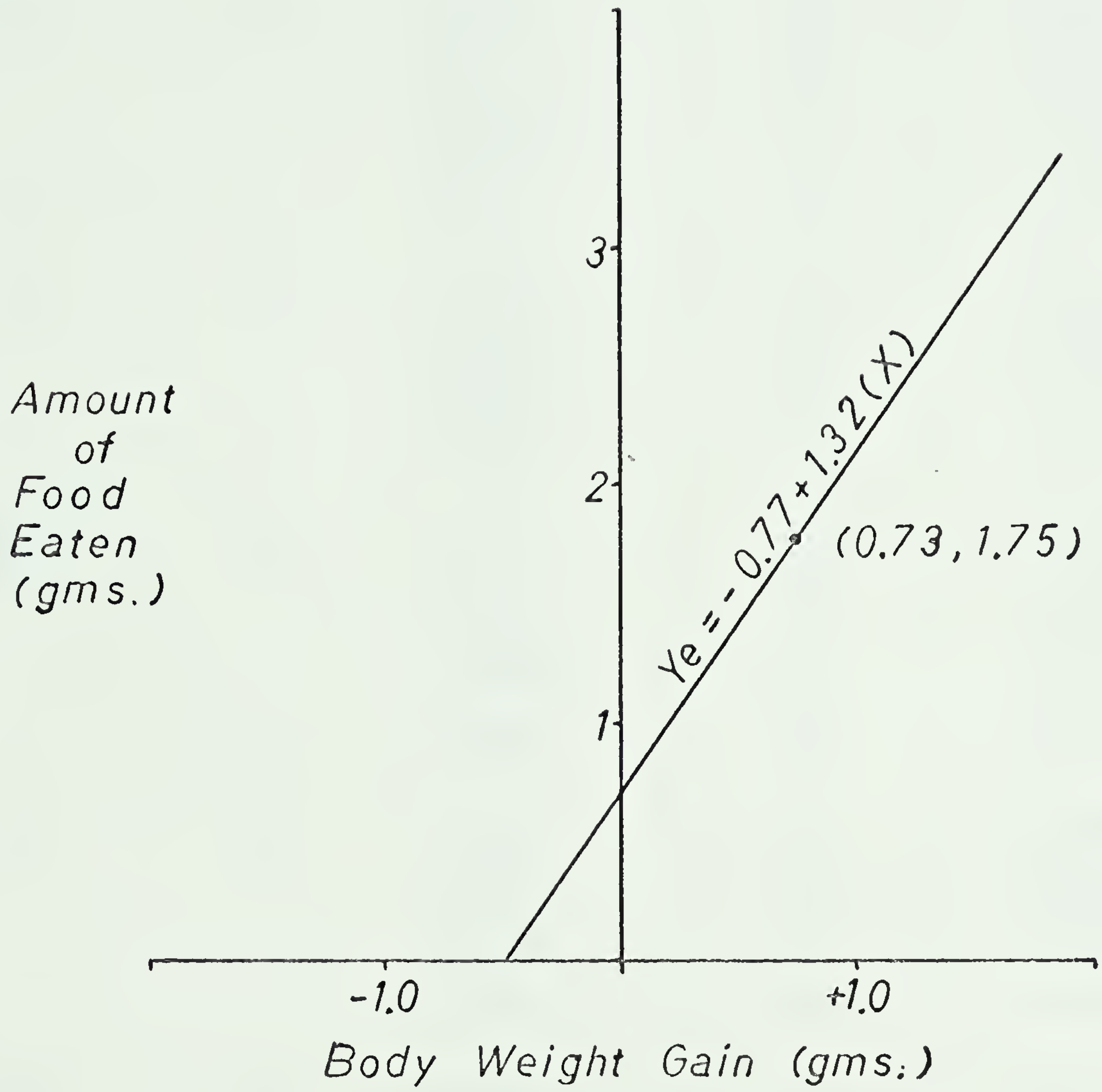

Figure 8. Regression of amount of food, Y on body weight change, X

Table 3 Mean number of feces of individual birds during total test periods in isolation

Design	Group no.	Bird	$\bar{X}$ no. of feces	$s_{\bar{x}}$	n *
I	2	Y-8	2	± 0.68	5
		G-7	2	± 0.51	5
		B-168	2	± 0.51	5
		C-9	2	± 0.73	5
I	3	Y-14	4	± 0.63	5
		G-12	3	± 0.45	5
		B-71	2	± 0.58	5
		C-15	4	± 0.40	5
II	4	Y-9	2	± 0.92	5
		G-8	1	± 0.37	5
		B-169	2	± 0.73	5
		C-10	2	± 0.51	5
II	5	Y-10	3	± 0.89	5
		G-9	1	± 0.63	5
		B-170	3	± 1.03	5
		C-11	3	± 0.20	5
II	6	Y-16	1	± 0.0	5
		G-14	2	± 0.32	5
		B-174	2	± 0.20	5
		C-17	2	± 0.87	5
III	7	Y-6	1	± 0.60	5
		G-5	2	± 0.71	5
		B-156	3	± 1.20	5
		C-7	1	± 0.24	5

Table 3 cont.

Design	Group no.	Bird	$\bar{X}$ no. of feces	$s_{\bar{x}}$	n *
III	8	Y-13	2	±0.58	5
		G-11	2	±0.37	5
		B-172	6	±0.58	5
		C-14	2	±0.58	5
III	9	Y-15	1	±0.56	5
		G-13	2	±0.55	5
		B-173	1	±0.00	5
		C-16	1	±0.40	5
III	10	Y-17	2	±0.51	5
		G-15	2	±0.49	5
		B-175	3	±0.40	5
		C-18	1	±0.40	5
IV	11	Y-7	2	±0.55	5
		G-6	1	±0.51	5
		B-157	2	±0.73	5
		C-8	4	±0.60	5

* n = Number of observations on each bird

Table 4 Estimation of basal metabolic rates of birds at beginning of test

Design	Group no.	Bird	Weight metabolism regression coefficient
I	1	Y-5	0.21
		G-4	0.22
		B-13	0.22
		C-5*	0.21
	2	Y-8	0.21
		G-7*	0.19
		B-168	0.21
		C-9	0.20
	3	Y-14*	0.20
		G-12	0.21
		B-71	0.20
		C-15	0.22
II	4	Y-9	0.24
		G-8	0.22
		B-169	0.22
		C-10*	0.24
	5	Y-10	0.20
		G-9	0.22
		B-170*	0.19
		C-11	0.22
	6	Y-16	0.21
		G-14*	0.23
		B-174	0.21
		C-17	0.21

Table 4 cont.

Design	Group no.	Bird	Weight metabolism regression coefficient
III	7	Y-6*	0.18
		G-5	0.17
		B-156	0.19
		C-7	0.20
	8	Y-13	0.19
		G-11*	0.21
		B-172	0.19
		C-14	0.23
	9	Y-15	0.20
		G-13	0.19
		B-173	0.22
		C-16*	0.20
	10 +	Y-17	0.17
		G-15	0.18
		B-175*	0.19
		C-18	0.19
IV	11	Y-7	0.20
		G-6	0.19
		B-157	0.20
		C-8*	0.20

* Bird which contributed greatest percentage to total agonistic encounters during tests

\+ The basal metabolic rates of the birds in this group were estimated by using body weights at beginning of 2nd test in group

Evaluation of Nervousness

Only the birds in two groups appeared to be exceptionally nervous. They were in Groups 5 and 6 in Design II excluding G-14 in Group 6.

Table 5 Record of ambient temperatures in ^{o}C during the tests

Design	Group	Day of test in group						Day of test in isolation				
		1	2	3	4	5	6	1	2	3	4	5
I	1	23.0	26.0	27.0	25.2	25.8	26.4	25.2	26.0	26.4	24.8	25.2
	2	22.0	24.0	21.5	23.3	23.0	23.0	23.0	22.0	23.5	23.0	22.5
	3	22.2	21.0	22.5	23.2	22.0	22.0	24.0	22.8	22.9	22.8	22.0
II	4	24.8	23.4	22.0	20.5	22.0	20.0	24.4	24.0	21.8	21.5	20.0
	5	23.0	23.0	23.5	23.5	23.0	23.0	24.0	23.0	25.0	23.0	22.9
	6	22.0	22.5	22.2	23.0	22.9	22.9	23.2	22.9	23.0	22.9	22.5
III	7	24.8	24.8	24.0	23.0	23.9	23.9	24.8	24.8	23.0	24.0	24.8
	8	22.0	24.0	21.5	23.3	23.0	23.0	23.0	22.0	23.5	23.0	22.5
	9	23.0	23.2	23.1	23.1	23.2	22.9	23.8	23.5	23.2	22.5	22.2
	10	23.0	22.9	22.5	22.7	23.0	21.9	22.9	23.0	22.9	22.9	23.1
IV	11	23.9	24.9	24.8	23.9	20.0	22.0	23.9	25.5	24.9	22.0	22.0

Description of agonistic behaviour observed

The encounters I observed during the tests which I interpreted as agonistic were:

actual peck;

One bird actually pecked the body of another. This was a sharper, more intense peck than a preening peck and usually was followed by retreat on the part of the pecked bird. During a preening peck the preened bird was usually stationary and it assumed a spherical posture, sometimes with its legs entirely tucked under it. At times its body feathers were fluffed a bit and the body appeared slightly puffed out. The bird receiving a preening peck did not retreat or try to avoid the bird that was doing the preening, but usually maintained the same posture after the preening peck.

I observed birds delivering these actual pecks on the head, wing, back, bill, and foot of another bird.

interrupted peck;

One bird attempted to peck the other bird but the latter successfully avoided the bill of the pecking bird, i.e. the peck was disrupted by the attacked.

intention movement of peck;

One bird would go through the action of a peck but would not make the effort to actually deliver the peck to the body of the other bird, i.e. the peck was disrupted by the attacker.

threat posture;

One bird would slightly crouch and stretch its head out towards the other bird. This usually elicited a retreat upon the part of the latter.

charging;

One bird would make a run at another bird, which usually elicited retreat on the part of the other bird.

jumping;

One bird would jump at another bird.

chasing and pursuit;

One bird would chase after the other bird.

feather pulling;

One bird would tug at the feathers of another.

leg pulling;

I observed leg pulling upon only one occasion. One bird pulled on the leg of another and made this other bird lose its balance.

pushing;

One bird would crowd out and shove another bird from the food or from some other spot in the cage.

"head turn";

Sometimes a dominant bird could displace another from the food container by turning its head toward the other bird.

vocal threat;

Upon occasion a dominant could displace a subordinate from the food by vocal threat alone.

submissive display;

I sometimes observed the subordinates of the monarchial dominant in Design III approach the localized food slowly, stealthily, and with their heads down. This I interpreted as submissive display.

giving way and avoidance behaviour;

One bird would leave a certain part of the cage as soon as another bird went there.

Text continued again on page 69.

Table 6 Categorization of dominance at individual level based on percentage individual bird won of the total agonistic encounters occurring in its group during the tests

Design	Group	Dominant	Subordinates			Total no. of agonistic encounters in all the tests
I	1	C-5 96%	Y-5 3%	G-4 1%	B-13 0%	92
	2	G-7* 60%	C-9 20%	Y-8 10%	B-168 10%	10
	3	Y-14 59%	B-71 28%	C-15 10%	G-12 3%	29
II	4	C-10 92%	Y-9 6%	B-169 2%	G-8 0%	48
	5	B-170* 83%	Y-10 8%	C-11 8%	G-9 0%	11
	6	G-14 60%	Y-16 24%	B-174 11%	C-17 1%	92
III	7	Y-6 100%	G-5 0%	B-156 0%	C-7 0%	465
	8	G-11* 75%	Y-13 12%	B-172 12%	C-14 0%	8

Table 6 cont.

Design	Group	Dominant	Subordinates			Total no. of agonistic encounters in all the tests
	9	C-16 74%	B-173 17%	G-13 4%	Y-15 4%	23
	10	B-175 100%	Y-17 0%	G-15 0%	C-18 0%	515
IV	11	C-8 68%	B-157 28%	G-6 4%	Y-7 0%	54

* The bird may or may not be the dominant

Table 7 Categorization of dominance at group level

Design no.	Group no.	% dominant in each group contributed to total agonistic encounters in that group	% agonistic encounters lost by dominant in each group	Detectable monarchial dominance Present	Trend	Absent
I	1	96%	0%	✓		
	2	60%	25%			✓
	3	59%	2%			✓
II	4	92%	2%		✓	
	5	83%	8%			✓
	6	66%	32%			✓
III	7	100%	0%	✓		
	8	75%	14%			✓
	9	74%	6%			✓
	10	100%	0%	✓		
IV	11	68%	27%			✓

Table 8 Reduced accessibility to food due to agonistic interactions

Mean no. of times individual bird displaced another from food or prevented another from reaching food

Design	Group	Dominant			Subordinates								
		$\bar{X}$	$s_{\bar{x}}$	n	$\bar{X}$	$s_{\bar{x}}$	n	$\bar{X}$	$s_{\bar{x}}$	n	$\bar{X}$	$s_{\bar{x}}$	n
I	1		C-5			Y-5			G-4			B-13	
		5.17	±0.98	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6
	2		G-7			Y-8			B-168			C-9	
		0.00	0.00	5	0.00	0.00	5	0.00	0.00	5	0.00	0.00	5
	3		Y-14			B-71			G-12			C-15	
		1.00	±0.52	6	0.50	±0.34	6	0.00	0.00	6	0.00	0.00	6
II	4		C-10			G-8			B-169			Y-9	
		3.33	±1.63	6	0.16	±0.16	6	0.00	0.00	6	0.00	0.00	6
	5		B-170			G-9			Y-10			C-11	
		0.00	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6
	6		G-14			Y-16			B-174			C-17	
		0.50	±0.34	6	0.00	0.00	6	0.00	0.00	6	0.17	±0.17	6
III	7		Y-6			G-5			B-156			C-7	
		25.2	±8.64	5	0.00	0.00	5	0.00	0.00	5	0.00	0.00	5
	8		G-11			Y-13			B-172			C-14	
		0.00	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6

Table 8 cont.

Design	Group	Dominant			Subordinates								
		$\bar{X}$	$s_{\bar{x}}$	n	$\bar{X}$	$s_{\bar{x}}$	n	$\bar{X}$	$s_{\bar{x}}$	n	$\bar{X}$	$s_{\bar{x}}$	n
	9		C-16			G-13			B-173			Y-15	
		0.00	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6
	10		B-175			Y-17			G-15			C-18	
		16.00	±3.62	5	0.00	0.00	5	0.00	0.00	5	0.00	0.00	5
IV	11		C-8			B-157			G-6			Y-7	
		2.17	±1.28	6	0.83	±0.83	6	0.00	0.00	6	0.00	0.00	6

n = Number of observations on same group

Figure 9 Despot of Group 7 displacing a subordinate from the food area in Design III

Figure 10 Despot of Group 7 displacing a subordinate from the food area in Design III while another subordinate approaches from another direction

Table 9 Evaluation of reduced accessibility of food as emphasized by dominance

Design	Group no.	Subordinate	Mean no. of times subordinate gained successful access to food* : mean number of times subordinate was prevented accessibility to food
I	1	B-13	3 : 2
		Y-5	4 : 1
		G-4	3 : 3
I	3	B-71	1 : 0
		G-12	1 : 1
		C-15	2 : 0
II	4	B-169	3 : 2
		Y-9	2 : 0
		G-8	4 : 2
III	7	B-156	0 : 16
		C-7	0 : 1
		G-5	0 : 8
III	10	Y-17	0 : 6
		G-15	0 : 7
		C-18	0 : 3
IV	11	B-157	2 : 1
		G-6	2 : 1
		Y-7	0 : 1

* See page 19 for definition of successful access to food

Table 10 Amount of food in grams eaten during the one hour test periods

Design	Group	Bird tag no.	$\bar{X}$ amt. of food eaten by ea. bird in isolation	s	n	$\bar{X}$ amt. of food eaten by ea. group in isolation	s	n	$\bar{X}$ amt. of food eaten by ea. group in group	s	n
I	1	Y-5	1.27	±0.71	5	6.47	±0.90	5	6.97	±1.64	6
		G-4	1.07	±0.87	5						
		B-13	2.39	±0.94	5						
		C-5*	1.73	±0.91	5						
	2	Y-8	1.16	±0.51	5	5.31	±2.44	5	4.71	±1.22	5
		G-7*	1.14	±1.09	5						
		B-168	1.75	±0.49	5						
		C-9	1.26	±0.74	5						
	3	Y-14*	3.25	±0.92	5	6.95	±1.59	5	7.15	±2.09	6
		G-12	0.76	±0.25	5						
		B-71	1.21	±0.60	5						
		C-15	1.54	±0.55	5						
II	4	Y-9	1.14	±0.38	5	5.12	±0.97	5	7.62	±1.96	6
		G-8	1.41	±0.32	5						
		B-169	1.97	±0.64	5						
		C-10*	0.60	±0.32	5						

Table 10 cont.

Design	Group	Bird tag no.	$\bar{X}$ amt. of food eaten by ea. bird in isolation	s	n	$\bar{X}$ amt. of food eaten by ea. group in isolation	s	n	$\bar{X}$ amt. of food eaten by ea. group in group	s	n
	5	Y-10	1.15	±0.87	5	5.16	±3.21	5	6.25	±2.50	6
		G-9	0.30	±0.42	5						
		B-170*	1.92	±1.03	5						
		C-11	1.79	±1.22	5						
	6	Y-16	1.22	±0.62	5	7.50	±3.40	5	8.05	±3.57	6
		C-14*	4.56	±1.71	5						
		B-174	1.27	±1.26	5						
		C-17	0.45	±0.76	5						
III	7	Y-6*	2.69	±2.07	5	7.77	±4.66	5	4.04	±3.49	5
		G-5	1.33	±0.90	5						
		B-156	2.28	±1.16	5						
		C-7	1.47	±1.19	5						
	8	Y-13	0.81	±0.31	5	6.61	±1.48	5	6.23	±1.70	6
		G-11*	2.21	±0.19	5						
		B-172	1.64	±0.64	5						
		C-14	1.95	±0.51	5						

Table 10 cont.

Design	Group	Bird tag no.	$\bar{X}$ amt. of food eaten by ea. bird in isolation	s	n	$\bar{X}$ amt. of food eaten by ea. group in isolation	s	n	$\bar{X}$ amt. of food eaten by ea. group in group	s	n
	9	Y-15	2.00	±1.06	5	6.13	±2.91	5	6.81	±1.75	6
		G-13	1.22	±0.65	5						
		B-173	1.26	±0.44	5						
		C-16*	1.65	±0.80	5						
	10	Y-17	2.02	±1.38	5	9.60	±3.54	5	5.97	±2.96	5
		G-15	2.48	±0.71	5						
		B-175*	2.75	±1.49	5						
		C-18	2.35	±0.72	5						
IV	11	Y-7	2.39	±0.89	5	10.32	±3.53	5	9.42	±2.95	6
		G-6	2.68	±1.11	5						
		B-157	2.34	±0.57	5						
		C-8*	2.91	±1.22	5						

* Bird which contributed greatest percentage to total agonistic encounters during tests

Analysis of amount of food eaten

Table 11 Analysis of amount of food eaten in Design III

Source of variation	df	SS	MS	F
Dom [a]	1	0.91	0.91	13.0
Rep (Dom)	2	0.14	0.07	
I[b] x Dom	1	21.72	21.72	54.30 *
Rep (Dom) x I	2	0.81	0.40	1
Rep (Dom) x Day (I)	12	21.85	1.82	
Dom x Day (I)	6	20.80	3.46	1.90
I	1	39.60	39.60	99.00**
Day (I)	6	96.78	16.13	8.86**

[a] Dom = Dominance category with two levels: 1) monarchial dominance detected and 2) not detected

[b] I = Feeding condition with two levels: 1) feeding in group and 2) feeding in isolation

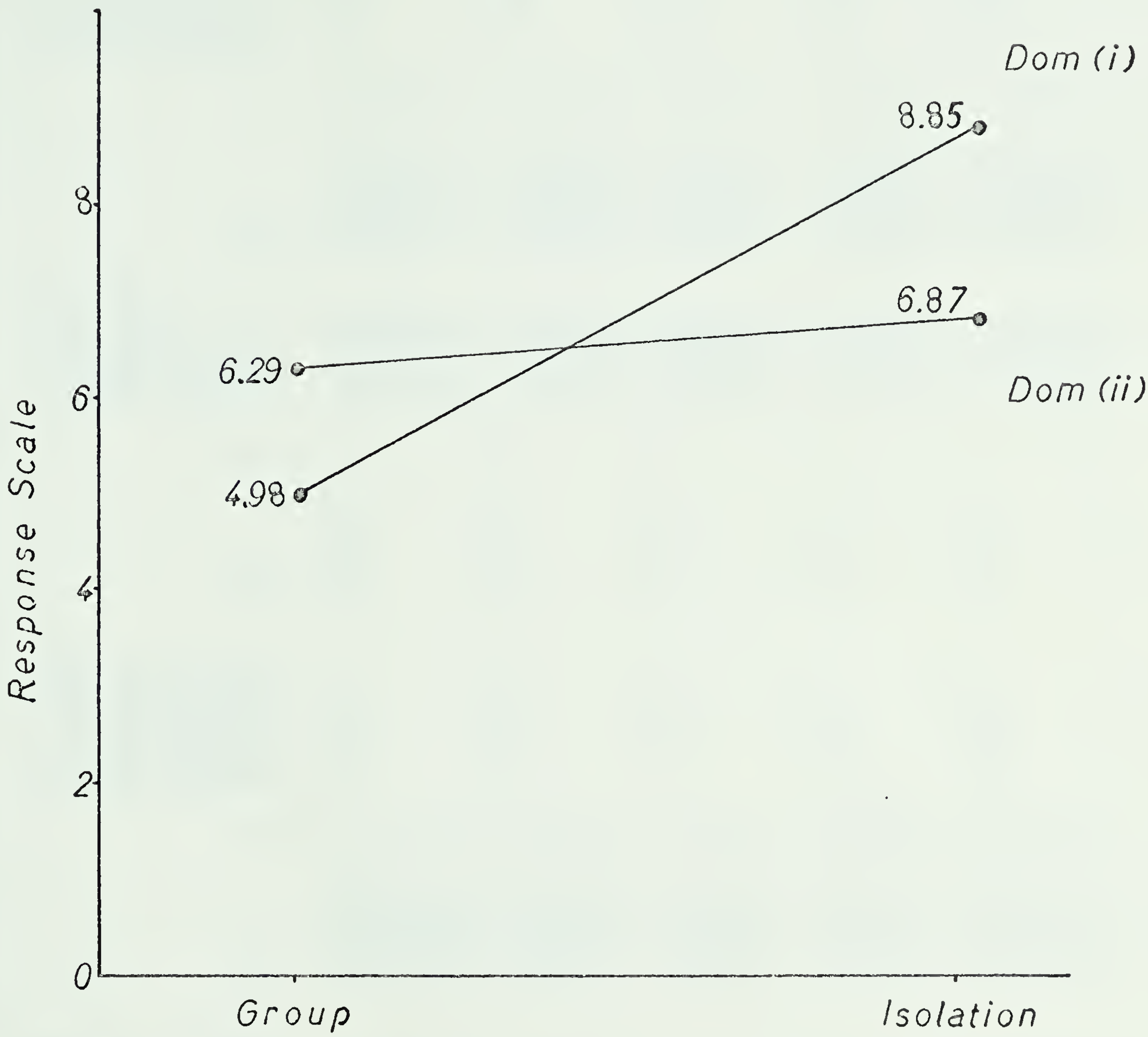

Figure 11. Feeding condition X dominance category interaction for the data on amount of food eaten. Dom (i): monarchial dominance detected, Dom (ii): monarchial dominance not detected.

Table 12 Body weight change in grams after one hour test periods

Design	Group	Bird tag no.	$\bar{X}$ body wt. change of ea. bird in isolation	$s_{\bar{x}}$	n	$\bar{X}$ body wt. change of ea. group in isolation	$s_{\bar{x}}$	n	$\bar{X}$ body wt. change of ea. bird in group	$s_{\bar{x}}$	n	$\bar{X}$ body wt. change of ea. group in group	$s_{\bar{x}}$	n
I	1	Y-5	±0.27	±0.42	5	+2.61	±0.54	5	+0.21	±0.18	6	+2.38	±0.58	6
		G-4	+0.17	±0.12	5				+0.15	±0.24	6			
		B-13	+1.39	±0.32	5				+1.36	±0.13	6			
		C-5*	+0.78	±0.13	5				+0.67	±0.12	6			
	2	Y-8	+0.48	±0.18	5	+1.88	±0.89	5	+0.22	±0.20	5	+1.00	±0.67	5
		G-7*	+0.15	±0.21	5				-0.03	±0.10	5			
		B-168	+0.72	±0.26	5				+0.44	±0.10	5			
		C-9	+0.53	±0.27	5				+0.37	±0.32	5			
	3	Y-14*	+2.28	±0.28	5	+2.95	±0.72	5	+1.96	±0.54	6	+2.72	±0.92	6
		G-12	-0.03	±0.11	5				-0.22	±0.15	6			
		B-71	+0.19	±0.10	5				+0.19	±0.09	6			
		C-15	+0.51	±0.29	5				+0.80	±0.27	6			
II	4	Y-9	+0.30	±0.19	5	+2.42	±0.54	5	+0.38	±0.13	5	+3.21	±0.45	5
		G-8	+0.97	±0.05	5				+0.78	±0.23	6			
		B-169	+1.06	±0.30	5				+1.56	±0.36	6			
		C-10*	+0.08	±0.14	5				+0.31	±0.10	6			
	5	Y-10	+0.51	±0.51	5	+2.11	±1.55	5	+0.22	±0.30	6	+1.92	±1.18	6
		G-9	-0.50	±0.19	5				+0.14	±0.23	6			
		B-170*	+1.02	±0.42	5				+0.74	±0.34	6			
		G-11	+1.08	±0.52	5				+0.82	±0.33	6			

Table 12 Cont.

Design	Group	Bird tag no.	$\bar{X}$ body wt. change of ea. bird in isolation	$s_{\bar{x}}$	n	$\bar{X}$ body wt. change of ea. group in isolation	$s_{\bar{x}}$	n	$\bar{X}$ body wt. change of ea. bird in group	$s_{\bar{x}}$	n	$\bar{X}$ body wt. change of ea. group in group	$s_{\bar{x}}$	n
	6	Y-16	-0.02	±0.14	5	+3.11	±1.44	5	+0.34	±0.12	6	+2.49	±1.35	6
		G-14*	+2.75	±0.75	5				+1.98	±0.65	6			
		B-174	+0.61	±0.61	5				+0.24	±0.39	6			
		C-17	-0.22	±0.24	5				-0.07	±0.43	6			
III	7	Y-6*	+1.04	±0.34	5	+2.71	±1.13	5	+0.62	±0.41	5	-0.13	±1.05	5
		G-5	+0.51	±0.29	5				-0.27	±0.25	5			
		B-156	+0.95	±0.34	5				+0.03	±0.37	5			
		C-7	+0.22	±0.30	5				-0.52	±0.08	5			
	8	Y-13	+0.12	±0.16	5	+2.28	±1.18	5	+0.05	±0.13	6	+1.88	±0.62	6
		G-11*	+0.77	±0.42	5				+1.10	±0.19	6			
		B-172	+0.60	±0.29	5				+0.61	±0.19	6			
		C-14	+0.79	±0.41	5				+0.12	±0.31	6			
	9	Y-15	+1.08	±0.56	5	+3.25	±1.19	5	+1.26	±0.40	6	+3.26	±0.88	6
		G-13	+0.55	±0.24	5				+0.73	±0.17	6			
		B-173	+0.51	±0.22	5				+0.40	±0.16	6			
		C-16*	+1.11	±0.32	5				+0.86	±0.22	6			
	10	Y-17	+0.59	±0.68	5	+4.44	±1.79	5	-0.11	±0.20	5	+2.17	±1.11	5
		G-15	+1.57	±0.19	5				+0.45	±0.24	5			
		B-175*	+1.07	±0.45	5				+1.23	±0.28	5			
		C-18	+1.20	±0.63	5				+0.61	±0.41	5			
IV	11	Y-7	+1.21	±0.41	5	+4.90	±1.57	5	+0.61	±0.31	6	+3.61	±1.06	6
		G-6	+1.35	±0.51	5				+1.98	±0.63	6			
		B-157	+0.86	±0.23	5				+0.22	±0.19	6			
		C-8*	+1.49	±0.53	5				+0.81	±0.07	6			

Analysis of body weight change

Table 13 Analysis of body weight change in Group 3, Design I

Source of variation	df	SS	MS	F
A^a	1	10.59	10.59	<1
b^b (A)	2	4,553.07	2,276.5	
A x P^c x G^d	1	12.03	12.03	1.52
b(A) x col.	38	299.31	7.87	

[a] A = Dominance category with two levels:
1) dominant
2) subordinate

[b] b = subjects

[c] P = Body weight of subjects with two levels: 1) body weight of subject before test and 2) body weight of subject after test

[d] G = Feeding condition with two levels: 1) feeding in group and 2) feeding in isolation

Table 14 Analysis of body weight change in Group 6, Design II

Source of variation	df	SS	MS	F
A[a]	1	4,649.04	4,649.04	3.70
b[b] (A)	2	2,493.74	1,246.87	
A x P[c] x G[d]	1	25.28	25.28	3.37
b (A) x col.	38	285.12	7.50	

a b c d See page 55

Table 15 Examination of the A x P x G interaction for the data of Table 16

	A1 (Dominant)			A2 (Subordinate)	
	P1 (pre-weight)	P2 (post-weight)		P1 (pre-weight)	P2 (post-weight)
G_1 (Group)	104.5	105.4	G_1 (Group)	104.2	104.2
G_2 (Isolation)	104.5	105.6	G_2 (Isolation)	103.3	104.2

Table 16 Analysis of body weight change in Groups 7 and 10, Design III

Source of variation	df	SS	MS	F
A[a]	1	25.37	25.73	<1
Gr[e] (A)	2	2,006.25	1,003.08	<1
b[b] (Gr)	4	4,637.69	1,159.42	
A x P[c] x G[d]	1	5.88	5.88	<1
Gr (A) x col.	30	84.74	2.82	<1
b (Gr) x col.	60	810.86	13.51	

a b c d See page 55

e Gr = Group

Table 17 Analysis of body weight change in Group 8, Design III

Source of variation	df	SS	MS	F
A^a	1	327.14	327.14	<1
b^b (A)	2	5,626.99	2,813.5	
A x P^c x G^d	1	4.04	4.04	<1
b (A) x col.	38	332.34	8.74	

a b c d See page 55

Table 18 Amount of time spent eating in seconds during one hour test periods

Design	Group	Bird tag no.	$\bar{X}$ amt. of time spent eating by ea. bird in isolation	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. group in isolation	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. bird in group	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. group in group	$s_{\bar{x}}$	n
I	1	Y-5	291	± 41.70	3	1464	± 30.44	3	354	±110.44	3	1352	±166.24	3
		G-4	158	± 23.68	3				175	±103.43	3			
		B-13	429	±186.54	3				251	± 47.56	3			
		C-5*	586	±172.10	3				572	±128.98	3			
	2	Y-8	239	± 94.99	5	584	±216.65	5	409	± 71.26	4	906	±188.16	4
		G-7*	72	± 24.87	5				88	± 25.39	4			
		B-168	170	± 72.51	5				188	± 52.51	4			
		C-9	104	± 30.77	5				222	± 56.78	4			
	3	Y-14*	a						452	± 94.36	6	1470	±342.71	6
		G-12	a						131	± 55.55	6			
		B-71	a			a			134	± 18.41	6			
		C-15	a						753	±208.06	6			
II	4	Y-9	168	± 38.53	4	973	±270.54	4	330	± 64.37	5	1842	±328.60	5
		G-8	450	±115.03	4				758	±146.80	5			
		B-169	244	± 93.05	4				424	±100.91	5			
		C-10*	111	± 30.74	4				330	± 47.69	5			

Table 18 cont.

Design	Group	Bird tag no.	$\bar{X}$ amt. of time spent eating by ea. bird in isolation	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. group in isolation	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. bird in group	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. group in group	$s_{\bar{x}}$	n
	5	Y-10	365	±209.06	5	742	±319.36	5	406	±138.57	6	896	±230.31	6
		G-9	31	± 28.86	5				158	± 31.24	6			
		B-170*	164	± 55.20	5				129	± 32.66	6			
		C-11	182	± 51.46	5				202	± 38.07	6			
	6	Y-16	a			a			120	± 32.92	5	1599	±620.71	5
		G-14*	a						904	±259.15	5			
		B-174	a						432	±247.37	5			
		C-17	a						143	±110.51	5			
III	7	Y-6*	1143	±448.33	5	2212	±701.83	5	1062	±429.55	5	1210	±489.23	5
		G-5	411	±164.52	5				60	± 52.40	5			
		B-156	278	±111.06	5				89	± 29.69	5			
		C-7	380	± 45.29	5				0	± 0.0	5			
	8	Y-13	a			a			142	± 36.22	6	1255	±307.12	6
		G-11*	a						241	± 36.38	6			
		B-172	a						153	± 65.96	6			
		C-14	a						720	±204.38	6			

Table 18 cont.

Design	Group	Bird tag no.	$\bar{X}$ amt. of time spent eating by ea. bird in isolation	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. group in isolation	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. bird in group	$s_{\bar{x}}$	n	$\bar{X}$ amt. of time spent eating by ea. group in group	$s_{\bar{x}}$	n
	9	Y-15	145	±59.39	5	1521	±520.18	5	157	±28.32	6	1363	±377.07	6
		G-13	178	±65.92	5				151	±36.59	6			
		B-173	585	±202.26	5				484	±154.92	6			
		C-16*	614	±220.27	5				571	±183.09	6			
	10	Y-17	a			a			108	±45.04	4	1241	±430.85	4
		G-15	a						426	±238.36	4			
		B-175*	a						607	±108.43	4			
		C-18	a						100	±59.88	4			
IV	11	Y-7	421	±143.78	5	1653	±311.56	5	199	±31.43	6	1765	±432.02	6
		G-6	219	±49.96	5				428	±153.42	6			
		B-157	374	±117.48	5				503	±153.27	6			
		C-8*	639	±49.94	5				635	±113.2	6			

* Bird which contributed greatest percentage to total agonistic encounters during tests

a Observations missing, see page 9

Analysis of time spent eating

Table 19 Examination of the A x G interaction for the data on time spent eating in Group 1, Design I

	Group	Isolation
A_1	1715	1757
A_2	780	878

Table 20 Analysis of time spent eating in Group 1, Design I

Source of variation	df	SS	MS	F
A[a]	1	411,324.00	411,324.00	7.55
b[b] (A)	2	109,016.00	54,508.00	
G[c]	1	2,450.00	2,450.00	<1
Day (G)	4	121,624.50		
A x G	1	3.93	3.93	<1
b (A) x col.	10	308,207.00	30,821.00	

[a] A = Dominance category with two levels: A1) dominant and A2) subordinate

[b] b = Subjects

[c] G = Feeding condition with two levels: 1) feeding in group 2) feeding in isolation

Table 21 Analysis of time spent eating in Group 6, Design II

Source of variation	df	SS	MS	F
A[a]	1	1,694,448.15	1,694,448.15	3.33
b[b] (A)	2	1,016,817.8	508,408.9	

a b See page 62

Table 22 Examination of the A x G interaction for the data of Table 23

	Group	Isolation
A_1 (Dominant)	5308	5714
A_2 (Subordinate)	248	1782

Table 23 Analysis of time spent eating in Group 7, Design III

Source of variation	df	SS	MS	F
A[a]	1	6,065,364.82	6,065,364.82	756.31**
b[b] (A)	2	16,039.34	8,019.67	
G[c]	1	282,427.17	282,427.17	11.90**
Day (G)	8	6,574,712.52	821,839.06	34.63**
A x G	1	95,351.74	95,351.74	4.02
b (A) x col.	18	427,136.73	23,729.82	

a b c See page 62

Table 24 Analysis of time spent eating in Group 9, Design III

Source of variation	df	SS	MS	F
A^a	1	537,474.68	537,474.68	1.28
b^b (A)	2	837,245.0	418,622.5	
G^c	1	99,360.08	99,360.08	2.46
Day (G)	8	2,150,825.48	268,853.18	6.66 **
A x G	1	14,322.68	14,322.68	<1
b (A) x col.	18	726,229.7	40,346.09	

a b c See page 62

Table 25 Analysis of time spent eating in Group 10, Design III

Source of variation	df	SS	MS	F
A^a	1	468,667.70	468,667.70	3.38
b^b (A)	2	277,240.17	138,620.08	

a b See a b page 62

Table 26 Analysis of time spent eating in Group 11, Design IV

Source of variation	df	SS	MS	F
A[a]	1	587,160.3	587,160.3	11.85
b[b] (A)	2	99,110.6	49,555.3	
G[c]	1	2,323.20	2,323.2	<1
Day (G)	8	709,730.10	88,716.26	2.53
A x G	1	3,370.8	3,370.8	<1
b (A) x col.	18	630,768.73	35,042.71	

a b c See page 62

Table 27 Level of agonistic behaviour expressed in the groups during the tests

Design	Group no.	Monarchial dominance Present	Trend	Absent	$\bar{X}$ no. of agonistic encounters occurring during tests	No. of test periods when no agonistic encounters were observed
I	1	✓			15.33	0
	2			✓	1.67	1
	3			✓	4.83	0
II	4		✓		8.00	0
	5			✓	2.00	0
	6			✓	15.33	0
III	7	✓			93.00	0
	8			✓	1.3	2
	9			✓	3.8	0
	10	✓			103.00	0
IV	11			✓	9.00	0

DISCUSSION OF RESULTS

Degree of relation between some of the variates measured

Body weight change and amount of food eaten are closely correlated, (Table 2, page 37). Ross and Ross (1949) also found similar results for two different breeds of puppies. The correlation coefficients for the two breeds were 0.97 and 0.99. They then used body weight change as an index of the amount of food eaten by the puppies in group. Tolman (1964) also used body weight change as an estimation of the amount of food eaten by domestic chicks. He did not, however, test how closely these two variables were correlated. Because the correlation coefficient which I calculated indicates that a close relationship exists between body weight change and amount of food eaten in isolation, I assumed that such a relationship also existed when the birds were fed in group, and used body weight change as an approximate estimation of the amount eaten by the individual birds in group.

Biometricians advise that it is risky to state that a close correlation exists unless the correlation coefficient is greater than 0.7, since often significant correlations are found which are meaningless. Therefore, although the correlation coefficient for time spent eating and amount of food eaten is significant (Table 2, page 37), I did not use time spent eating as an index of

the amount of food eaten. It is easily understandable why time spent eating is not as good an index of the amount of food eaten as body weight change, since different amounts of food can be eaten in the same amount of time, if feeding is at different rates.

Number of feces / hour test and body weight change are not significantly correlated, (Table 2, page 37). Hence individual differences in body weight change recorded during the tests cannot be significantly attributable to individual differences in defecation rate.

Ambient temperature

I did not find any literature on the thermoneutral range for Japanese quail but the thermoneutral range for domestic fowl was reported to be 18-26°C by Barott and Pringle (1946) and 16-35°C by Spector (1956) and I assumed that the thermoneutral range for quail should be somewhat similar. Since the temperatures recorded during the tests ranged from 20-27°C (the temperature was 27° on only one day), I do not think that ambient temperature was an important extraneous variable in my tests.

Agonistic behaviour observed during the tests

Farris (1964) also observed actual pecking, charging, threat posture and retreat in Japanese quail. He noted too vocal threat in adult males.

Whenever I recorded feather pulling, it occurred in what I interpreted to be agonistic context.

I tallied the one incidence of leg pulling I observed as an agonistic encounter. There is a possibility, nevertheless, that this might not have been such, since I did not record whether C, the bird that had its leg pulled out, ran away after it regained balance, or whether it assumed some sort of submissive attitude or retaliated. The bird who did the leg pulling, G, had, however, just pecked C before it pulled C's leg out, which suggests an agonistic context.

Evaluation, categorization and description of dominance

At individual level

Groups 2, 5 and 8 were asterisked in Table 6, page 46, as I was not certain if the bird I categorized as dominant actually was the dominant, since the total number of agonistic encounters that occurred during the tests was only approximately 10 which may not be adequate to evaluate dominance at the individual level.

At group level

According to my categorization, monarchial dominance was found in three groups and in one group a trend towards this type of hierarchy was detected (Table 7, page 47). These findings concur with Farris (1964) who also found monarchial dominance in groups of quail of mixed sex. Selinger, Howard and Bermont (1967) and Sachs (1966), however, found bidirectional dominance in paired male quail. I also found bidirectional dominance in some

of my groups and so it would appear that this type of hierarchy also occurs in female quail. It may be, however, that this bidirectional dominance is a transitional period preceding the establishment of monarchial dominance. My results thus indicate that neither monarchial dominance nor bidirectional dominance is the one given social hierarchy that occurs in all groups of quail all of the time. Urich (1938) also found this to be the case in white mice. Although he found that monarchial dominance was the most common type of social hierarchy in these animals, he states that his study clearly demonstrates that their social hierarchy is by no means the same in all groups or even in the same group all of the time.

Dominance and reduced accessibility to food

The dominant bird was virtually always the one which displaced another from the food or prevented another from reaching the food (Table 8, page 48). Whether or not this displacing of one bird from the food by another or preventing another to reach the food was active defence of the food, is difficult to ascertain, especially in the Designs where the food is dispersed. In these Designs, it may have just been solely dominance being expressed and that expression had to take place somewhere in the cage. As food was placed in all corners of the cage in the "food-dispersed Designs" and as the birds spent a lot of their time in the corners of the cage (even when the food

was absent during the deprivation period), there is a good probability that expression of dominance would have taken place at the food.

In Groups 7 and 10 of Design III, however, where the dominant displaces the subordinates from the food or prevents them from reaching the food, it may be less risky to interpret this as defence of food since most of the interactions took place at the site of the localized food as opposed to any other place in the cage. Upon occasion, the dominant would leave the food area and the subordinates would immediately go there and begin to eat. The dominant would then quickly go back to the food and displace the subordinates.

Inter-group, intra-design comparison

By making an intra-design comparison, the effect of pure dominance on reduced accessibility to food is most clearly seen, since in such a comparison any effect of Design that might influence dominance is held constant.

In Design I, Group 1, where monarchial dominance had been detected, the despot displaced its subordinates and prevented them from reaching the food a greater number of times than did the dominants of the other groups in this Design, where monarchial dominance had not been detected. The subordinates' accessibility to food, however, was not reduced to a greater extent in Group 3 where monarchial dominance had not been found as compared with Group 1 where it had (Table 9, page 50).

In Design II when Group 4, where a trend toward monarchial dominance was detected, is compared to Groups 5 and 6, where a trend was not obvious, it is seen that the dominant in the former group displaced its subordinates and prevented them from reaching the food a greater number of times than the dominants in the latter groups (Table 8, page 48).

In Design III a marked difference is noticeable between the Groups 7 and 10, where monarchial dominance was detected and Groups 8 and 9, where it was not. In the latter case, no displacements from the food took place and no bird was prevented from reaching the food during all the tests. In contrast is the former case where the despots in the groups displaced and prevented the subordinates from reaching the food to such an extent that the subordinate birds did not once attain successful access to food during the tests (Tables 8 and 9, pages 48,50). Figures 9 and 10 (page 49) show the monarchial dominant Y-6 of Group 7 displacing its subordinates from the food area. Figure 10 illustrates how the dominant had to attempt "simultaneous" defence, i.e., defending the food area from more than one approaching subordinate at a time.

Scott (1950) states that the essential feature of an aggressive food competition seems to be a conflict between fear of despot and degree of hunger. In Groups 7 and 10, the subordinates would continue to approach the food in spite of previous aggressive displacements by the

dominant. This suggests that hunger rather than fear may possibly be the stronger drive in this food competition conflict.

Inter-group, inter-design comparison

If Group 1 in Design I (detectable monarchial dominance present) is compared to Groups 7 and 10 in Design III (detectable monarchial dominance also present) (Table 9, page 50), it can be noted that reduced accessibility to food as emphasized by dominance is greater in Design III. This would seem to be accounted for by the different arrangement of the food in the two Designs (dispersed in Design I vs. clustered in Design III). When the dominant displaced a subordinate from the food in Design I, the subordinate would often go to a food dish at another corner of the cage and be undisturbed by the dominant. Thus, although the subordinate was prevented accessibility to food in one part of the cage where the dominant was, it was still able to gain accessibility to food in another part of the cage. This was not possible in Design III, where the food was localized in one small area.

As the monarchial dominant in Group 1 dominated 96 per cent of the total agonistic encounters that occurred, as compared to 100 per cent by the monarchial dominants in Groups 7 and 10, it could be argued that the monarchial dominants are stronger in Groups 7 and 10 and that is why accessibility to food was more greatly reduced

due to dominance in Design III. A point against this argument is that the evaluations of dominance in the groups were made on the basis of agonistic interactions observed when the groups were in the Designs, and since the Designs might possibly influence the expression of dominance, it could be that monarchial dominance in Group 1 would be more strongly expressed if this group were Design III.

Evidence to indicate that the arrangement of the food is, at least, partly responsible for the difference in reduced accessibility to food as emphasized by dominance is brought forward by the results of Supplementary Test No 2 (pages 98-100). In the three tests when the birds were in Design III, all the subordinates would approach the food and B-175, the despot already at the food would displace them. The subordinates would approach the food again and the dominant would displace them again. However, when the birds were in Design II "a food-dispersed Design", only one of the subordinates Y-17 approached the food where B-175 was, B-175 displaced it and Y-17 then withdrew and fed at another food container away from B-175 and did not approach B-175 again during the remainder of the test. The other subordinates ate at food containers apart from the dominant and did not approach the dominant at all.

In making an inter-design comparison of the groups in which monarchial dominance was not detected, it is seen that Design does not seem to have any great effect on

reduced accessibility to food as emphasized by dominance (Tables 8, 9, pages 48, 50). Only one possible exception was in Group 11. Y-7 did not once attain successful accessibility to the food during the tests and it could be the nature of the feeding Design that was responsible for this, although other factors also could have been involved.

Amount of food eaten

Inter-group, intra-design comparison

Design I

The amount of food eaten by Group 1, where monarchial dominance was detected, was approximately the same in group as in isolation, as was also the case for Groups 2 and 3, where monarchial dominance was not detected. This is compatible with the results for these Groups on reduced accessibility to food as emphasized by dominance (Table 9, page 50). In Group 1, the monarchial dominant did not reduce its subordinates' access to food to any greater extent than did the non-monarchial dominant in Group 3.

It would seem that this Design provided a situation where the negative effects of group feeding on food consumption tend to be minimized, since the subordinates could avoid the dominant and still feed.

Design II

Group 4 ate a greater amount in group than in isolation and I also observed that these birds were more active in group than in isolation. This may have possibly been the phenomenon of "social facilitation" (i.e. the

expression of the positive effects of group on food consumption) which is known to occur in animals feeding together in a situation where the effects of competition are minimized. The amount eaten in group as compared with isolation was not so great in Groups 5 and 6. The birds in these Groups were very nervous and many times when one bird was feeding and another bird would start to move around excitedly, the bird feeding would stop and also run around in a very excited manner. This did not occur in isolation. I interpreted this behaviour to be contagious behaviour which is defined by Scott (1950) as that "in which the activity of any individual stimulates similar activity on the part of another. The response of the latter may in turn act back on the first animal. The reaction is circular and as a result is intensified and may spread throughout the group." Fear is seen to be contagious in a flock of sheep or in a herd of cattle (Scott, 1950). There may have been a passive component involved in the situation described in Groups 5 and 6, i.e. one bird may have been pushed by another, which action may have triggered a response rather than stimulated it. However, upon some occasions I did observe a bird excitedly running about and then another beginning to act similarly without any tactile provocation. In Group 6, one bird G-14, did not appear to be excited when the others were, but tried to feed while they ran about. When they would do this, however, they spent most of their time running to and fro

along the back of the cage where G-14 was trying to feed, running over or under G-14 and interrupting its feeding. Thus it was seen how a group could have negative effects on its own food consumption that was not directly related to dominance or competition.

Design III

It was found by factorial analysis that the interaction between kind of hierarchy, (monarchial dominance detected vs. not detected) and feeding situation, (group vs. isolation) was statistically significant, (Table 11, page 52). In Groups 7 and 10, where monarchial dominance was detected, the amount of food consumed in group was less than in isolation, whereas in Groups 8 and 9, where monarchial dominance was not detected, the amount consumed in group was about the same as in isolation. This is not surprising in view of the results on reduced accessibility to food as emphasized by dominance, (Table 8, page 48). The non-monarchial dominants appeared to be much more tolerant than the monarchial dominants and the former always fed side by side with their subordinates. This was rarely the case with the monarchial dominants who most often prevented their subordinates from even reaching the food.

Taking all the groups into consideration a significantly greater amount was eaten in isolation than in group (Table 11, page 52). Ross and Ross (1949) predicted this when they suggested that effects on feeding

other than "facilitating" would probably be found if animals were fed in a competitive situation.

The amount of food eaten on different days was also significant. Two interpretations apropos this result were discussed on page 5, viz. conditioning to a rhythm or the effect of familiarization.

Design IV

In Design IV Group 11 ate slightly more in isolation than in group. Although this Design, of all the Designs was intended to most favor reduced accessibility to food, defence of food and any negative effects of a group on its own food consumption, a comparison of the observations on Group 11 and on the Groups in Design III does not demonstrate this.

The birds in Group 11 fed side by side many times without any displacements from the food resulting. This was in contrast to Groups 7 and 10 of Design III. The difference between Groups 8 and 9, and 7 and 10 in Design III as well as the results of Supplementary Test No. 3 (pages 101-105) indicate that the difference in behaviour and hence in amount of food eaten between Group 11 of Design IV and Groups 7 and 10 of Design III is more likely to be attributable to a difference in the Groups' characteristics rather than to a difference in these two Designs.

Inter-design comparison

In Design III it was seen that the interaction between dominance category and feeding condition was statistically significant. Although a factorial analysis was not possible in Design I, it can be seen that all three Groups ate about the same in isolation as in group in spite of one group's having detectable monarchial dominance present while the other two Groups did not. My observations during the tests as well as the data on reduced accessibility to food as emphasized by dominance (Table 9, page 50) suggest that the different results on the amount of food eaten in Design I and III may be largely attributable to the difference in the arrangement of food in the two Designs, (dispersed vs. clustered). Orgain and Schein (1953) inferred that the distribution rather than the quantity of food was directly controlling the number limit of rats in a colony and suggested that if food is more widely distributed, then food consumption will be increased in a colony.

Body weight change

Intra-group, inter-group, intra-design comparison

Design I

In Design I, the monarchial dominant in Group 1 and the non-monarchial dominant in Group 2 did not gain more weight than their subordinates (Table 12, page 54), whereas the non-monarchial dominant in Group 3 did, (although not significantly) (Table 13, page 55).

Although the monarchial dominant displaced its subordinates from the food a greater number of times than did the non-monarchial dominants (Table 8, page 48), it appears that the monarchial dominant did not have a greater advantage over its subordinates in terms of body weight gain than the non-monarchial dominants, which was probably because of the dispersed arrangement of the food in this Design. Often when the monarchial dominant would displace its subordinates from a food dish they would go to another, apart from the dominant bird, and feed. As body weight gain is a correlate of the amount of food eaten in isolation and is probably also a good index of the amount eaten by each individual bird in group, it would seem that in a Design where the food is dispersed, the monarchial dominant does not necessarily consume more food than its subordinates.

Design II

The dominant in Group 4 which showed the greatest trend towards a monarchial dominance hierarchy did not have a greater advantage over its subordinates with respect to body weight gain than did the non-monarchial dominants in Groups 5 and 6. In this Design the food was also dispersed, and as was the case in Design I, subordinates, when displaced from one food dish by a dominant, would often go to another dish and feed.

In Group 6 the dominant G-14 did gain more weight, although not significantly, than its subordinates (Table 12, page 54). Why this was so may possibly be because this dominant was the only bird in the group that would settle down during the test period. The others appeared more nervous and spent a lot of time moving excitedly about the cage while G-14 fed. In turn, one possible reason why G-14 would settle down during the test period and feed could have been that G-14 had a slightly higher Basal Metabolic Rate than the other birds (Table 4, page 40) and perhaps the 18-hour food deprivation before the tests had a greater effect on G-14. It has been noted in ground squirrels that dominants are frequently "bolder" than subordinates and less easily disturbed (A.L. Steiner, personal communication) and this also appears to have been true of the dominant G-14.

Design III

Both monarchial dominants in Design III gained more weight, although not significantly, than their respective subordinates during the tests in group and also in isolation. The Basal Metabolic Rates of these dominants, however, is not higher than their subordinates (Table 4, page 40) which suggests that their greater body weight gain during the tests is not directly related to their Basal Metabolism. A trend was found for both the monarchial dominants in Design III to gain more weight than their

respective subordinates when they were in group than when they were in isolation. However, this trend (the A x P x G interaction) was not significant when it was tested statistically (Table 16, page 58).

This may be because this difference was too small to be significantly detected by the number of observations made.

Another possible interpretation is that the lack of significance is really a negative result and that the difference in body weight gain, and therefore probably in the amount of food eaten, between the monarchial dominants and their respective subordinates is not greater in group than in isolation. For, although the monarchial dominants did reduce their subordinates' accessibility to food to a certain extent (Table 8, page 48), the subordinates, nevertheless, approached the food again and again and ate, in spite of being frequently displaced. Sabine (1959) observed in the field that subordinates in a winter society of Oregon juncos persistently returned to the food tray although they were pecked by dominants there. He suggests that this is why during one particularly bitter winter when food was scarce, he did not note that the low ranking birds were especially prone to starvation.

In Group 8 where monarchial dominance was not detected, G-11 gained more weight, although not significantly, than the other birds in the group. However as previously discussed (page 71) G-11 may not be the

dominant bird in the group. At any rate I did not observe any agonistic behaviour on the part of this bird during the test that would account for its gaining more weight than the others.

The non-monarchial dominant in Group 9 did not gain more weight than its subordinates which is not surprising since it did not once displace the subordinates from the food (Table 8, page 48).

Design IV

I hypothesized that Design IV would be the one Design wherein the dominant would have the greatest advantage over its subordinates with respect to body weight gain, as compared to the other Designs, since I expected the clustered arrangement of food plus restricted cage size would best facilitate defence of food. However, the dominant C-8 in Group II did not gain more weight than its subordinates. This may have been because monarchial dominance was not present in Group II and I observed C-8 to be much more tolerant of its subordinates at the food than the monarchial dominants of Groups 7 and 10 in Design III (Tables 8 and 9, pages 48 and 50).

Time spent eating

As I found in my study that time spent eating was not closely correlated with amount of food eaten, as was body weight change, it is not very surprising that in some groups a dominant which spent the most time eating,

did not gain the most weight, or vice versa when compared to its subordinates.

Intra-group, inter-group, intra-design comparison

Design I

In Group 1, Design I, the monarchial dominant C-5 spent more time eating, though not significantly more (Table 20, page 62) than its subordinates during all the test periods, both in group and in isolation, but there was not very much of a trend toward this difference being greater in group than in isolation (Table 19, page 61). Hence, the reason why C-5 spent the most time eating has probably not related to some factor present only in the group situation. Neither was the reason why C-5 spent the most time eating that C-5 had a higher Basal Metabolic Rate than its subordinates (Table 4, page 40).

The non-monarchial dominants of Groups 2 and 3 in Design I did not spend more time eating than their respective subordinates. This was in accordance with my observations during the tests, as I did not note any behavioural interactions that would favor the dominants spending the most time eating.

Design II

The dominants in Groups 4 and 5 also did not spend more time eating than their respective subordinates, even though the dominant in Group 4 was a strong one and showed a trend toward being a monarchial dominant. In these

Groups, as well, I did not observe any behavioural interactions that would favor the dominants spending the most time eating.

In Group 6, where no monarchial dominance was detected, the dominant, G-14 spent more time eating in group than its subordinates, (although not significantly more). One possible reason why G-14 tended to spend the most time eating was that the bird was noticeably less nervous than the others in the group. While the others spent a lot of time moving about excitedly in the cage, G-14 was feeding. This difference in individual nervousness in Group 6 has previously been discussed on pages 78, 79, and 83.

Since no data could be recorded on time spent eating in isolation for this group (see page 9), the A x G interaction, i.e. the interaction between rank of bird, whether dominant or subordinate, and feeding situation, whether in group or isolation, could not be tested.

Design III

In Group 7 of Design III the monarchial dominant spent significantly more time eating than its subordinates during all the test periods, in isolation as well as in group (Table 23, page 65). Although there was a trend towards the difference between time spent eating by the dominant and subordinates to be greater in group than the difference between these same birds in isolation (Tables 22 and 23, pages 64, 65) this trend, i.e. the A x G interaction,

was not significant. However, it was almost significant ($F = 4.02$, $F_{.05} = 4.41$) and it may be that with more replications it would have been. The subordinates tended to spend less time eating than the dominant in group because the dominant continually displaced them from the food.

There was significantly more time spent eating in isolation than in group by Group 7 as a whole (Table 23, page 65). Also the effect of days was significant, i.e. there was more time spent eating during the later tests than during the former tests. This may have been partly due to a conditioning or a "familiarization effect" discussed on page 5.

In Group 9 the non-monarchial dominant C-16 spent slightly more time eating than its subordinates (Table 24, page 66). When these birds were isolated the difference in time spent eating between C-16 and its subordinates was greater than when they were together; so this along with my observations suggest that why C-16 spent more time eating was not related to some factor present in the group alone.

In Group 10 although the monarchial dominant did spend more time eating than its subordinates, this was not significant (Table 25, page 66) unlike in Group 7 where it was. This may have been because the difference was not great enough to be detected by the number of replications made. In Group 10, unlike Group 7, no results were

recorded during the test days in isolation (page 9), and also in Group 10, one less day was recorded in the group situation (page 4) than in Group 7.

Another interpretation might be that the lack of significance in Group 10 is truly a negative result and there was no real difference between the time spent eating by the dominant and subordinates in Group 10. If this were the case, it may be that the hunger drive of the subordinates in Group 10 is stronger than the fear drive to a greater extent than is the hunger drive of the subordinates in Group 7.

Design IV

In Group 11 the dominant C-8 did spend more time eating than its subordinates but this was not significant (Table 26, page 67). This may possibly be related to the absence of detectable monarchial dominance in this group as is discussed on page 85.

Intra-group, inter-design comparison

A trend towards the difference between time spent eating by the monarchial dominant and its subordinates to be greater in group than when these birds were in isolation was seen in Group 7 in Design III (probability = 6%, Tables 22 and 23, pages 64, 65) but not in Group 1 in Design I (Tables 19 and 20, pages 61, 62). Although this could be due to individual differences in these two groups' characteristics, my observations during the tests suggest

that it was rather due to the different arrangement of the food in the two Designs. In Design I the subordinates did not have to approach the dominant to feed, but if they did and were displaced from the food, they could still feed in other corners of the cage away from the dominant. This was not possible in Design III where the food was localized in one corner of the cage.

Expressed Level of Agonistic Behaviour

Inter-group, intra-design comparison

Design I

In Group 1 where monarchial dominance was detected there was a higher mean number of agonistic encounters than in Groups 2 and 3, where monarchial dominance was not detectable, (Table 27, page 68). This suggests that more tolerance exists in a group where monarchial dominance is absent or where the hierarchy is so settled that monarchial dominance, although present, is not able to be detected.

Design II

Although there was a greater trend toward monarchial dominance in Group 4 than in Group 6, there was a higher mean number of agonistic encounters in Group 6 during the tests. This may possibly be explained by the "frustration" which may have existed in Group 6. Many, many times when G-14 tried to eat, the other birds would run excitedly back and forth over and under G-14 and

interrupt its feeding. G-14 used to respond by pecking these birds and at times the other birds pecked back. In Group 4 such a situation did not exist.

Design III

In this Design there was a great difference between the level of agonistic encounters between Groups 7 and 10, where monarchial dominance was detected and Groups 8 and 9, where it was not detected (Table 27, page 68). In Group 8 there are even two test periods where no agonistic encounters occurred at all. Again these results suggest that more tolerance exists in a group where monarchial dominance is absent or where the situation is so settled that monarchial dominance appears to be absent.

Inter-group, inter-design comparison

An inter-design comparison of the groups with detectable monarchial dominance shows that the mean number of total agonistic encounters occurring during the tests is greater in Groups 7 and 10, which were in Design III than in Group 1, which was in Design 1. This could be due to a difference between Group 1 and the other two Groups, but my observations during the tests suggest that it is more likely due to the difference in the arrangement of food containers in these two Designs, (dispersed in Design I vs. clustered in Design III). Although the despots in all three groups spent most of their time at the food, the subordinates could avoid the dominant and

still feed in Design I, whereas this was not possible in Design III where the food was localized in one corner. In Design III, the subordinates had to approach the dominant to feed and agonistic encounters resulted.

Andrew (1957) compared feeding tests of one, and two food containers placed far apart, in a flock of yellow hammers and found that the level of aggressiveness was much lower in the two dish situation. In Andrew's tests the quantity as well as the accessibility of food were manipulated at the same time. In Design I and III, however, only accessibility to food was changed and there still was a lower level of agonistic behaviour in the situation where accessibility was made greater by dispersing the food containers.

SUMMARY

The main results obtained in the different Designs are summarized below:

In Designs I and II, where the food containers were dispersed in the corners of the cage, presence or absence of monarchial dominance did not seem to have a decremental effect on the total amount of food eaten by the group. The monarchial dominants did not gain more weight than their respective subordinates. Although the monarchial dominants displaced their respective subordinates from the food a greater number of times than the non-monarchial dominants did, the subordinates of the former did not appear to eat less, as they had the possibility to feed at other dishes apart from the dominant.

In Design III, where the food containers were concentrated in one corner of the cage, there was an obvious difference between feeding in groups with monarchial dominance and in groups without. In the former case, the birds consumed more in isolation than they did in group, whereas in the latter case the birds ate approximately the same in isolation as in group. The monarchial dominants gained more weight and spent more time eating than their respective subordinates and there was a trend for this difference between monarchial dominants

and subordinates to be greater in group than when these birds were isolated. The monarchial dominants displaced their subordinates from the food a greater number of times than did the non-monarchial dominants. In the groups where no monarchial dominance was detected, subordinates often fed side by side without any agonistic encounters resulting, which was in contrast to the situation in groups where monarchial dominance was present.

In Design IV, where access to the food was most restricted, it was hypothesized that competition would be potentially maximum (i.e. if monarchial dominance was present). However, due to the random assignment of groups to the Designs, only groups without monarchial dominance were tested in this Design. The results obtained did not differ greatly from those obtained with groups without monarchial dominance in Design III.

Results on the level of agonistic behavior in all these Designs suggest that there was more tolerance exhibited in groups without monarchial dominance than in groups with monarchial dominance.

Although it has been shown that feeding in group can have an incremental effect ("social facilitation"), some of the results obtained in this study indicate that feeding in group can have a decremental effect on food consumption by all or some of the members of the group.

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APPENDIX

Supplementary tests:

Supplementary Test No. 1

Introduction and methods

Because I observed that the birds in both Groups 1 and 2 in Design I spent more time eating at the food containers at the back of the cage than at those at the front, I thought that the birds might eat more if I put two extra food containers at the back of the cage in the arrangement as diagrammed on page 33, i.e. in the arrangement of Design II. In an attempt to evaluate this hypothesis, I subjected Group 2 on its Group Test Day No. 6 to a one hour feeding test in Design II. Up to this day Group 2 had been tested in Design I. The mean amount of food eaten in group in Design I is compared with the amount eaten during this one hour test in Design II in Table 28, page 98.

Results of Supplementary Test No. 1

Table 28 Mean amount of food eaten by Group 2 in Design I as compared with Design II

Design	$\bar{X}$ amt. of food eaten by Group 2 in group	$s_{\bar{x}}$	n *
I	4.71	± 1.22	5
II	9.05	-	1

* n = Number of observations on Group 2

Discussion of Supplementary Test No. 1

The results of this test suggest that Design II may favor greater food consumption than Design I. In Design II the birds had more opportunity to feed at the back of the cage where they were farther away from the observer and other visual disturbances outside their cage during the test.

Supplementary Test No. 2

Introduction and method

Part of my general procedure for all the tests was to take the food from the birds after the one hour test period was over. I then gathered up the scattered grains and weighed the food, and approximately one hour and forty five minutes passed before the birds were given food again. As a supplementary test I observed Group 10 in Design III for five minutes after I had given the food back, i.e. after they had been deprived of food for one hour and forty five minutes on these group test days. I recorded the agonistic behaviour I observed. On Group 10's last test day in group in Design III I put the food containers in Design II arrangement for this five minute supplementary test, to compare it with the three previous tests in Design III.

Table 29 Summary of agonistic encounters - Supplementary Test No. 2

Design	Day of test in group	No. of pecks	No. of other agonistic encounters	No. of times dominant displaced another bird or prevented another from reaching the food
III	2	82	3	7
III	3	9	2	5
III	4	15	0	6
II	5	0	1	1

Discussion of Supplementary Test No. 2

The results of this test seem to indicate that the arrangement of the food has an important influence on the expressed level of agonistic behaviour in a group, i.e., the clustered arrangement of food containers tends to increase the expressed level of agonistic behaviour.

Supplementary Test No. 3

Introduction and method

A greater level of agonistic behaviour was detected in Groups 7 and 10 of Design III than in Group 11 of Design IV, although Design IV had been set up to be the most competitive of all the Designs. I hypothesized that this was because of a difference in the groups' characteristics, since Groups 8 and 9 in Design III also exhibited a lower level of agonistic behaviour than Groups 7 and 10. And in an attempt to test this hypothesis I subjected a group of four birds, Group 12, to: four consecutive test days in group in Design IV (Round I); four consecutive test days in group in Design III; and then four consecutive test days in group in Design IV again (Round II). On all the days, the birds were deprived of food 18 hours prior to the one hour test. As I originally intended this Group for another test, two days preceding the beginning of testing in Design IV (Round I), I subjected this Group to 24 hours of food deprivation, then one day preceding Design IV (Round I), I subjected it to 20 hours of food deprivation.

Results of Supplementary Test No. 3

Table 30 Evaluation of dominance at individual level in Group 12

Design	Percentage individual bird contributed to total agonistic encounters during the test				Total no. of agonistic encounters during the tests
	C-12	B-171	G-10	Y-11	
IV (Round I)	34%	65%	2%	0%	139
III	88%	0%	0%	12%	8
IV (Round II)	64%	0%	36%	0%	11

Table 31 Evaluation of dominance at group level in Group 12

Design	% of total agonistic encounters occurring in the group during all the tests that dominant bird dominated	% of total agonistic encounters occurring during the tests which directly involved the dominant bird which the dominant bird lost	Monarchial dominance		
			Present	Trend	Absent
IV (Round I)	65%	23%			✓
III	88%	12%			✓
IV (Round II)	64%	0%			✓

Table 32 Level of agonistic interactions occurring during Supplementary Test No. 3

Design	Mean frequency of total agonistic encounters	$s_{\bar{x}}$	n*	Mean no. of times one bird prevented another from reaching the food or displaced another from the food	$s_{\bar{x}}$	n*
IV Round I	347.0	± 18.29	4	7.0	± 2.48	4
III	2.0	± 0.82	4	0	0	4
IV Round II	2.8	± 0.63	4	0	0	4

* n = Number of observations on Group 12

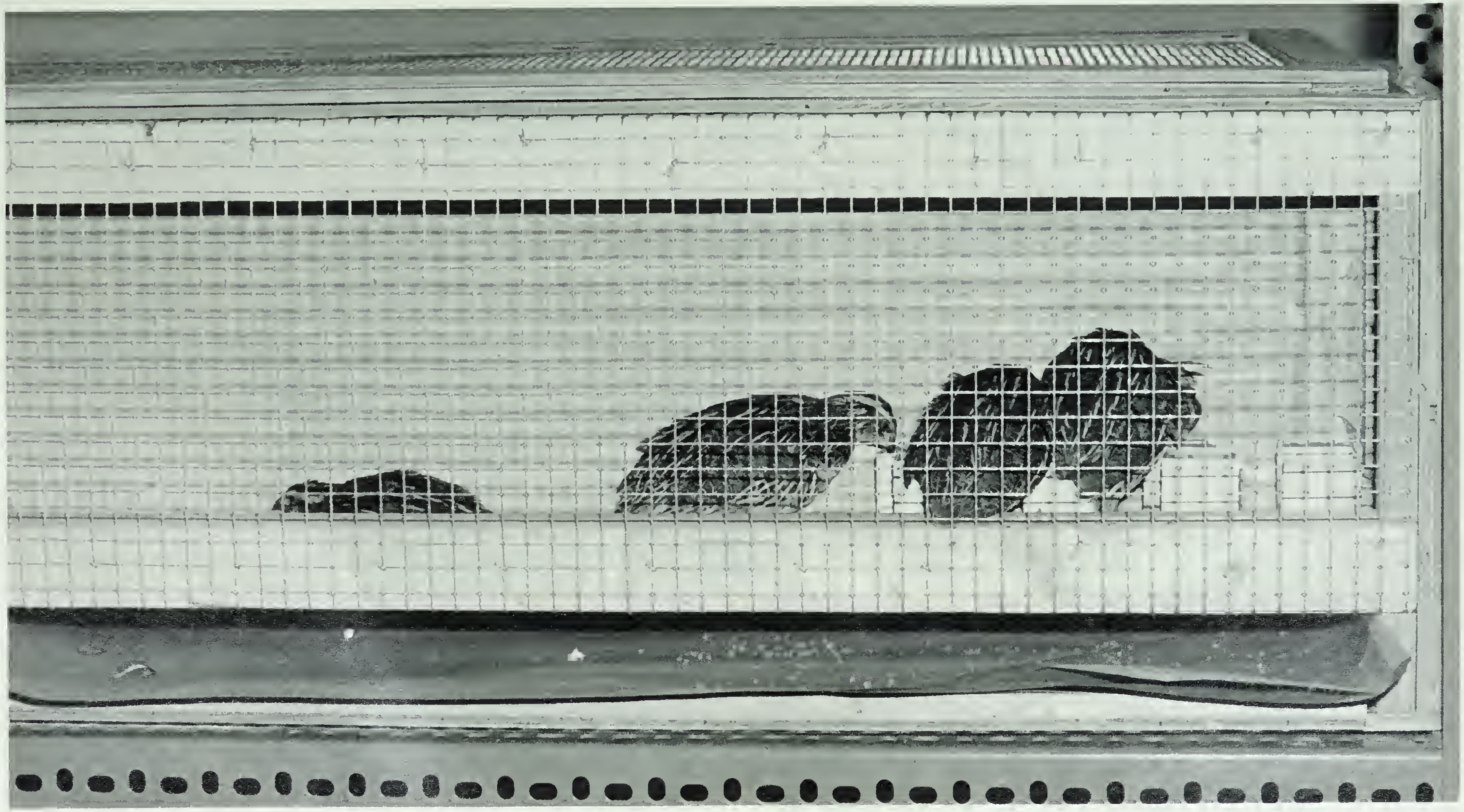

Figure 12 Group 12 in Design IV

Discussion of Supplementary Test No. 3

Monarchial dominance was not detected in Group 12, (Tables 30 and 31, page104)There was a greater mean level of agonistic behaviour in Design IV (Round I) than in Design III, but the level was approximately the same in Design IV (Round II) as in Design III (Table 30, page 104). The greater level in Design IV (Round I) may be related to the Group's having been deprived 24 and 20 hours on the two days preceding the commencement of the test. Figure 12 illustrates how the birds in Group 12 could crowd together at the food in Design IV without aggressive displacements resulting.

The results of this test seem to indicate that the great difference between the level of agonistic behaviour in Groups 7 and 10 of Design III, and Group 11 of Design IV was more likely to be attributable to a difference in the Groups' characteristics than to a difference in the two Designs and that when monarchial dominance is not detectable the level of agonistic behaviour is not greatly increased in Design IV over that in Design III.